JOURNAL

OF THE

ARNOLD ARBORETUM

Vol. XLI | October 1960 | Number 4

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, I.

FOLIAR VASCULATURE OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

I. W. Bailey

The tribe Pereskieae Britt. & Rose of the subfamily Pereskioideae K. Schum. has long been considered to contain the less specialized representatives of the Cactaceae, i.e., as regards possessing normal leaves and a characteristic dicotyledonous woody habit of growth. Since the publication of Berger's (1926) "Die Entwicklungslien der Kakteen," *Pereskia sacharosa* Griseb. and *P. aculeata* Mill. have been regarded, primarily upon the basis of floral evidence, as the most primitive members of the tribe and therefore of the Cactaceae as a whole (Buxbaum, 1953).

If the normal leaf-bearing cacti are to be utilized as an initial fundamental basis in studying salient trends of phylogenetic specialization within the Cactaceae, and in obtaining evidence of valid taxonomic, physiological and ecological significance, it is essential that both the exomorphic and the endomorphic structures of all organs and parts of *Pereskia* (including *Rhodocactus*), *Pereskiopsis* and *Quiabentia* be thoroughly investigated.

The simple, entire leaves of these genera vary markedly in size and form, not only in different putative species, but also at times in the same clone when grown under different environmental influences (e.g., wild *vs.* cultivated plants), and not infrequently in different parts of a single plant. The thickness of fully matured leaves appears to be somewhat more nearly stabilized at times within species, certain of the pereskias having relatively thin laminas in contrast to the more or less exaggerated succulence of others and particularly of various species of *Pereskiopsis* and *Quiabentia*. It is of interest to determine whether there are endomorphic structures within the leaves which are of reliable taxonomic utility in the differentiation of taxa, particularly genera and tribes. In clearing and sectioning leaves for microscopic examination, I have encountered differences in patterns of venation that appear to be of some significance in this connection.

Especially in the case of foliar succulence, critical details of vasculature are more or less obscure in superficial examination of leaves both from living plants and from herbarium specimens. Adequate clearing of such leaves involves more serious difficulties than I have encountered in dealing with the foliage of other families of the dicotyledons. Simple prolonged treatments with sodium hydroxide, lactic acid, chloral hydrate and other clearing reagents are unsatisfactory, maceration and disintegration of the lamina tending to occur before clearing is adequate. Successive, brief, carefully controlled treatments in 3% sodium hydroxide at 56° C., chloral hydrate, and, where essential, with hydrochloric acid or ferric chloride for the removal of superabundant crystals of calcium oxalate have yielded sufficiently clear preparations for the study of venation in most cases. However, the cleared leaves are so fragile that they must be handled with great care. All of the illustrations in PLATES IV–VI were made from unstained leaves mounted in diaphane.

In the leaves of 33 putative species from which I have succeeded in obtaining evidence, the foliar vasculature varies from dominantly pinnate (FIG. 25) to palmate or radiate (FIG. 26).

SPECIES WITH DOMINANTLY PINNATE VENATION

The leaves of *Pereskia aculeata* Mill., *P. bahiensis* Gürke, *P. bleo* DC., *P. corrugata* Cutak, *P. cubensis* Britt. & Rose, *P. portulacifolia* Haw., *P. grandifolia* Haw., *P. moorei* Britt. & Rose, *P. sacharosa* Griseb. (including *P. amapola* Web. and *P. argentina* Web.), *P. tampicana* Web. and *P. zinniifolia* DC. have a broad, conspicuous midvein which subtends an embossed costa on the abaxial or lower surface of the leaf.[1] In these leaves of typically pinnate vasculature, the comparatively tenuous principal lateral veins extend diagonally outward from contact with the midvein toward the margins of the lamina where they interconnect by curvatures of a "camptodrome" pattern. The details of the vasculature vary somewhat in leaves of different sizes and forms, the narrower and more extensively elongated leaves having more numerous lateral veins than do the proportionally broader and shorter forms. (Compare FIGS. 1 and 2.) The characteristically small leaves of *P. cubensis* (FIG. 4) and *P. portulacifolia* (FIG. 3) have a less conspicuously embossed costa in the upper part of the lamina.

In the case of *Pereskia colombiana* Britt. & Rose, *P. diaz-romeroana* Cárd., *P. guamacho* Web., *P. humboldtii* Britt. & Rose, and *P. weberiana* K. Schum., the 4–6 lateral veins which diverge from the midvein in the basal half of the lamina commonly tend to be conspicuous and extensive in contrast to the tenuous shorter ones in the upper part of the leaf (FIGS. 5–9). These extensive basal lateral veins frequently tend to run more nearly parallel to the contour of the margins of the lamina rather

[1] Illustration (Britton & Rose, *fig. 4,* 1919) of the imperfectly known *P. lychnidiflora* DC. suggests that it may likewise belong in this category of putative species.

than abruptly and diagonally toward them. (Compare Figs. 1 and 9.) The leaves of these putative species are quite variable in size and form. In the case of *P. guamacho*, where the general range of variability in size and form is quite similar to that in *P. colombiana*, some of the leaves, at least at times, have a pseudo-palmate venation as illustrated in Fig. 6.

SPECIES WITH PSEUDO-PALMATE TO PALMATE [2] VENATION

In available material of *Pereskiopsis chapistle* Britt. & Rose, *P. kellermanii* (Rose) Britt. & Rose, *P. rotundifolia* (DC.) Britt. & Rose, *P. scandens* Britt. & Rose and *P. velutina* Rose, there are 3, 5, 7 or 9 conspicuous veins. The extensively arcuate lateral veins usually extend independently of the slender midvein from the base of the leaf toward its apex (Figs. 17–21). Each of the lateral veins subtends a more or less conspicuously embossed costa on the abaxial or lower surface of the lamina, at least during certain stages of the maturation of the leaf. The lateral veins on each side of the midvein commonly tend to be aggregated slightly above the base of the leaf. In the case of *P. chapistle*, *P. porteri* and *P. velutina*, of which I have several collections both from wild and cultivated plants, the venation remains typically palmate regardless of variations in the size and form of the leaves (Figs. 17, 18, 20, 21).

In available material of *P. aquosa* (Web.) Britt. & Rose, *P. blakeana* Ortega, *P. gatesii* Baxter, and *P. diguetii* Britt. & Rose, the lateral veins frequently, but not invariably, tend to diverge from contact with the midvein above the base of the leaf (Figs. 14, 22) and therefore are pseudo-palmate rather than truly palmate. The thick, extremely succulent leaves of *Quiabentia pereziensis* Backbg. (Fig. 33) and *P. zehntneri* (Britt. & Rose) Britt. & Rose (Fig. 24) have a venation that varies from palmate to pseudo-palmate.

The leaves of *Pereskia pititache* Karw., *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. are extraordinarily variable in form on shoots of the same plant (Figs. 10–13, 15–16). The venation varies from pseudo-palmate to palmate. It is significant that the leaves of these putative pereskias differ from those of all other investigated species of *Pereskia* (with the exception of an occasional leaf of *P. guamacho* [Fig. 6]) in having a venation which resembles that of *Pereskiopsis* and *Quiabentia* rather than a dominantly and characteristically pinnate one.

PRELIMINARY OBSERVATIONS UPON THE MICROSCOPIC STRUCTURE OF VEINS, VEINLETS AND LEAF TRACES

Although the patterns formed by the minor veins and veinlets vary considerably, as illustrated in Figs. 27–32, fundamentally similar ones occur in the three genera *Pereskia, Pereskiopsis* and *Quiabentia*. (Com-

[2] As defined by Asa Gray (1880) palmately or radiately veined leaves have "three, five, seven or nine ribs which spread from the top of the leaf-stalk and run through the blade like the toes of a web-footed bird."

pare Figs. 25, 26.) In these genera the veins, veinlets and the ends of the veinlets are composed of tracheary cells with helical and annular thickenings. The phloem fibers which cap the leaf traces in the stem do not extend outward into the lamina of the leaf (except in rare instances), but are replaced by elongated parenchymatous elements of a pseudo-collenchymatous nature. Nor are there sclereids, either free in the mesophyll or jacketing the veins or veinlets, such as occur at times in xerophytic species of other dicotyledonous families.

Where the veinlets are comparatively slender, as commonly in the large thin leaves of various pinnately veined pereskias (Fig. 27), they may be composed largely of a single linear series of tracheary cells which become shorter in the terminal parts of the veinlets (Fig. 33). Where the terminal parts are coarser (Figs. 28, 29) as commonly occurs in more succulent leaves, the tracheary cells tend to be more numerous and more nearly isodiametric (Fig. 34). In the case of the coarsest patterns of vasculature (Figs. 30, 31) the veinlets, as well as their terminal parts may be composed of, or jacketed by, short tracheary cells (Fig. 36).

Although patterns of veinlet vasculature may ultimately prove to be of some taxonomic significance in the differentiation of taxa (e.g., in the case of species of *Quiabentia*; compare Figs. 31, 32) much more extensive collections of the leaves of different species must be secured and studied than are available at present. This is due to there being considerable variation in the details of vasculature in different leaves of the same clone and at times in those of the same plant. Furthermore, it should be emphasized in this connection that it is essential to compare the vasculature of fully matured leaves, for more or less extensive changes in details of venation occur during the enlargement and expansion of the lamina of immature leaves.

The curious short, wide cells with broad, annular thickenings which have attracted so much attention in literature dealing with highly specialized representatives of the Cactaceae (e.g., Schleiden, 1845; van Tieghem, 1885; Darbishire, 1904) do not occur in any of the pereskias of which I have adequate material. On the contrary, they appear sporadically in the leaves and stems of various putative species of *Pereskiopsis*. Such cells and their possible precursors are of common and abundant occurrence in the basal parts of the leaves of *Quiabentia pereziensis* Backbg. and *Q. zehntneri* (Britt. & Rose) Britt. & Rose. In the leaves of these plants, the veins are composed of broader tracheary cells with coarser thickenings than are those of *Pereskia* and *Pereskiopsis*. (Compare Figs. 35 and 37.) The cells on the margins of the veins have very broad helical and annular thickenings which project deeply into the lumina of the cells. There are transitions between elongated forms of such tracheary cells and very short ones with a few annular thickenings. Such transitional forms suggest that the short, broad elements which occur in other cacti may have evolved by modification of ordinary tracheary cells with helical or annular thickenings.

The midvein of pereskias which have pinnate venation is not a simple structure, but is composed of discrete vascular strands aggregated in an arc, i.e., as seen in transverse sections of the lamina (FIGS. 45–47). The vascular arc varies considerably in form and size in leaves of different dimensions. In the base of some leaves close to their level of attachment to the stem, the arc is so extensive that it forms a nearly or completely closed cylinder (FIG. 48). The number of constituent vascular strands likewise varies, not only in leaves of different sizes, but also at different levels of the same lamina, i.e., tending to increase in number from the apex of the leaf toward its base (FIGS. 44–48). It is evident from cleared leaves and from serial transverse sections at successive levels of the lamina that such a midvein is constituted of *two* aggregations, the individual vascular strands of which extend diagonally outward into the longitudinal halves of the lamina.

The individual strands of the vascular aggregate in the midvein may fuse or divide in various parts of their longitudinal extension (FIGS. 44, 47). When such changes occur the behavior of the xylem and phloem frequently is not closely synchronized. During fission, the separation of strands of phloem usually precedes division of the xylem. Conversely during fusion concrescence of the xylem is precocious. The collenchymatous parenchyma commonly caps the strands of phloem (FIGS. 45–47) but may at times form a continuous layer over the entire abaxial surface of the arc of vascular strands.

The number of discrete strands at any particular level of the leaf may be an *even* or an *odd* one. It is significant in this connection, however, that in a majority of cases there is no conspicuous larger strand which occupies a median position in the arc of discrete bundles. Instead of this there commonly are two aggregates of strands on either side of a more or less conspicuous median parenchymatous gap (FIGS. 45–47). In the case of *Pereskiopsis*, the slender midvein of palmately veined leaves not infrequently is composed of two discrete strands at least in parts of its extension (FIG. 43). Similarly the terminal part of the midvein in the apex of pinnately veined leaves may be composed at times of two more or less closely approximated strands (FIG. 44).

This evidence suggests from a phylogenetic point of view that, as in the case of Austrobaileyaceae, Trimeniaceae, Monimiaceae, Chloranthaceae and certain other families, the longitudinal halves of the lamina of *Pereskia*, *Pereskiopsis* and *Quiabentia* are vascularized by branches of two independent systems of leaf traces rather than by dichotomies of a single trace (Bailey, 1956). According to this view, the simple midvein which occurs at times in *Pereskiopsis* and *Quiabentia*, and the presence in some cases of a medianly placed strand in the arc of bundles of pinnately veined pereskias, is due phylogenetically to the fusion of branches of two independent systems or to asymmetries and the displacement of a single branch into a median position.

If such an interpretation is valid, additional evidence should be ob-

tainable from nodal and subnodal parts of the stem. The node of the leaf-bearing cacti is a consistently unilacunar one. In stems of *Pereskia aculeata*, and at least in parts of those of such species as *P. autumnalis*, *P. diaz-romeroana*, *P. guamacho* and *P. nicoyana* there commonly are two discrete leaf-traces at the nodal level (FIGS. 38, 39). These traces can be followed downward in serial transverse sections, or in adequately cleared stems, for considerable distances below the node. In the case of *Pereskia sacharosa*, *P. grandifolia*, *P. bleo* and in certain stems of *Pereskiopsis*, there may be four (FIG. 40), six (FIG. 41), or more traces (FIG. 42) at the nodal level, such differences being correlated at least to a certain extent with variations in the size of the leaves, with variations in the diameter of stems to which the leaves are attached, or with combinations of such factors. The alternating phyllotaxy is so complex ($\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$) that it is difficult to follow these vascular strands downward in the same orthostiche. However, in favorable cleared stems of *Pereskiopsis* it is possible to determine that the vascular strands frequently connect with two traces which may fuse for a varying distance and then diverge to *two* above the subtending leaf of the same orthostiche, where they connect with the traces of two separate adjacent orthostiches.

The totality of available evidence indicates that the vasculature of the leaf-bearing cacti presents varying phylogenetic modifications of a fundamentally two-trace unilacunar structure (Bailey, 1956). It is evident that apparent fission of vascular strands may occur at various levels of the stem, node and leaf. Furthermore, various asymmetries and aberrant fusion or division of vascular strands can lead at any given level to the appearance of an *odd* rather than an *even* number of vascular bundles.

More extensive investigation of nodal anatomy and of the form of the midvein in pinnately veined pereskias might eventually yield some evidence of taxonomic utility. But, as in the case of patterns formed by minor veins and veinlets, the range of structural variation in a single species, clone or plant is frequently so obvious that extensive collections must be studied before valid conclusions can be attained.

DISCUSSION

In the discussion of plant taxa and their relationships, evidence from similarities should be harmonized with that obtained from dissimilarities. In the case of the leaf-bearing cacti the similarities are so numerous in various organs and parts that it raises some question regarding the wisdom of placing putative genera in separate subfamilies or tribes. As regards leaves, the ranges of variability in a single clone (and not infrequently in a single plant) are so extensive that they necessitate a re-examination of putative species based in the past upon assumed differences in the size or external form of the foliar appendages. As I have shown, there are transitions in the leaf-bearing cacti between dominantly pinnate and typically palmate venation. Although the foliage of *Pereskiopsis* and *Quiabentia* appears to be dominantly pseudo-palmate or palmate, it does

not differ consistently from that of *Pereskia* (including *Rhodocactus*), since similar venation occurs in *Pereskia autumnalis*, *P. conzattii*, *P. nicoyana* and *P. pititache*. Such species as *P. colombiana*, *P. diaz-romeroana*, *P. guamacho*, *P. humboldtii* and *P. weberiana* have a venation which appears to be transitional between that of the preceding species and those which have a dominantly pinnate venation. Pseudo-palmate and palmate venation is correlated with increasing succulence of the leaves. This suggests, but, by itself without corroborative evidence, does not conclusively prove, that the evolutionary transition is from pinnate to palmate.

It is evident thus far in my preliminary anatomical investigations that there are at least four categories of putative species of leaf-bearing cacti which differ more or less markedly in their foliar vasculature. It will be of interest in subsequent anatomical investigations to determine whether there are other anatomical differences in these categories of species which correlate with those of the foliar vasculature. In so doing, it will be desirable, if possible, to determine whether the similarities within each category are due solely to close genetic relationship or in part to parallel evolutionary changes.

The objection may be raised that it is difficult and uncertain to determine the identity of plants from which material is collected in gardens and in the wild. This is particularly the case at present in dealing with species. However, the possibility of misidentifications does not modify the conclusion that there are four categories of leaf-bearing cacti with differing foliar vasculature.

The two-trace unilacunar vasculature and its various modifications in leaf-bearing cacti is significant in any general discussion of the possible relationships of the Cactaceae to other families of the dicotyledons and particularly to those of the Centrospermae.

ACKNOWLEDGMENTS

This investigation was financed by a grant from the National Science Foundation. I am indebted to the Arnold Arboretum, the Gray Herbarium, the N. Y. Botanical Garden, the Smithsonian Institution and the Chicago Natural History Museum for the loan of herbarium specimens. In addition, I am greatly indebted to the following individuals for their laborious and coöperative efforts in collecting adequately preserved specimens: N. Boke, M. Cárdenas, R. Romero Castañeda, A. Castellanos, I. D. Clement, L. Cutak, R. L. Dressler, Gates Cactus Inc., E. Hernandez, P. C. Hutchison, M. Kimnach, R. M. King, H. E. Moore, Jr., R. Moran, H. F. L. Rock, R. L. Rodríguez, A. J. Sharp, W. L. Stern, J. A. Steyermark, and H. Teuscher.

LITERATURE CITED

BAILEY, I. W. 1956. Nodal anatomy in retrospect. Jour. Arnold Arb. 37: 269–287.

BERGER, A. 1926. Die Entwicklungslinien der Kakteen. Gustav Fischer, Jena.

BRITTON, N. L., and J. N. ROSE. 1919. The Cactaceae. Vol. I. Carnegie Inst. Washington.

BUXBAUM, F. 1953. Morphology of Cacti. Sect. II. The flower. Abbey Garden Press. Pasadena, Calif.

DARBISHIRE, O. V. 1904. Observations on *Mamillaria elongata*. Ann. Bot. 18: 375–416.

GRAY, A. 1880. Lessons in Botany. Ivison, Blakeman, Taylor & Co. New York.

SCHLEIDEN, M. J. 1845. Beiträge zur Anatomie der Cacteen. Mém. Acad. Imp. Sci. St. Petersbourg 4: 335–380.

TIEGHEM, P. VAN. 1885. Valeur morphologique des cellules annelées et spiralées des Cactées. Bull. Soc. Bot. France 32: 103–106.

EXPLANATION OF PLATES

The source of the material figured for each species is given in brackets following the name. A complete listing of materials with all available documentary data will be given at the end of this series of papers.

PLATE I

FIGS. 1–9. LEAVES OF PERESKIA. All leaves drawn natural size. 1, *P. sacharosa* Griseb. [Mo. Bot. Gard.]; 2, *P. aculeata* Mill. [*Moran 7272*]; 3, *P. portulacifolia* (L.) Haw. [*Jiménez 2578*]; 4, *P. cubensis* Britt. & Rose [Atkins Gard.]; 5, *P. weberiana* Schum. [*Cárdenas*]; 6, *P. guamacho* Web. [*Steyermark*]; 7, *P. colombiana* Britt. & Rose [*Record 16495*]; 8, *P. diaz-romeroana* Cárd. [*Cárdenas*]; 9, *P. guamacho* Web. [*Steyermark*].

PLATE II

FIGS. 10–16. LEAVES OF PERESKIA AND PERESKIOPSIS. All leaves drawn natural size. 10, *Pereskia conzattii* Britt. & Rose [*Kimnach 172*]; 11, *P. pititache* Karw. [Atkins Gard.]; 12, *P. autumnalis* (Eichlam) Rose [*Moore*]; 13, *P. nicoyana* Web. [*Rodríguez 662*]; 14, *Pereskiopsis blakeana* Ort. [*Kimnach 81*]; 15, *Pereskia pititache* Karw. [Atkins Gard.]; 16, *P. autumnalis* (Eichlam) Rose [*Moore*].

PLATE III

FIGS. 17–24. LEAVES OF PERESKIOPSIS AND QUIABENTIA. All leaves drawn natural size. 17, 18, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [17, N. Y. Bot. Gard.; 18, *Moran 7349*]; 19, *P. scandens* Britt. & Rose [N. Y. Bot. Gard.]; 20, 21, *P. chapistle* (Web.) Britt. & Rose [20, *Hernandez*; 21, N. Y. Bot. Gard.]; 22, *P. aquosa* (Web.) Britt. & Rose [N. Y. Bot. Gard.]; 23, *Quiabentia pereziensis* Backbg. [*Cárdenas*]; 24, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE IV

FIGS. 25, 26. CLEARED LEAVES OF PERESKIA AND PERESKIOPSIS. 25, *Pereskia cubensis* Britt. & Rose [Atkins Gard.], × 5.5. 26, *Pereskiopsis velutina* Rose [Mo. Bot. Gard.], × 5.5; two dark-colored tips of glochids are embedded in the cleared lamina.

PLATE V

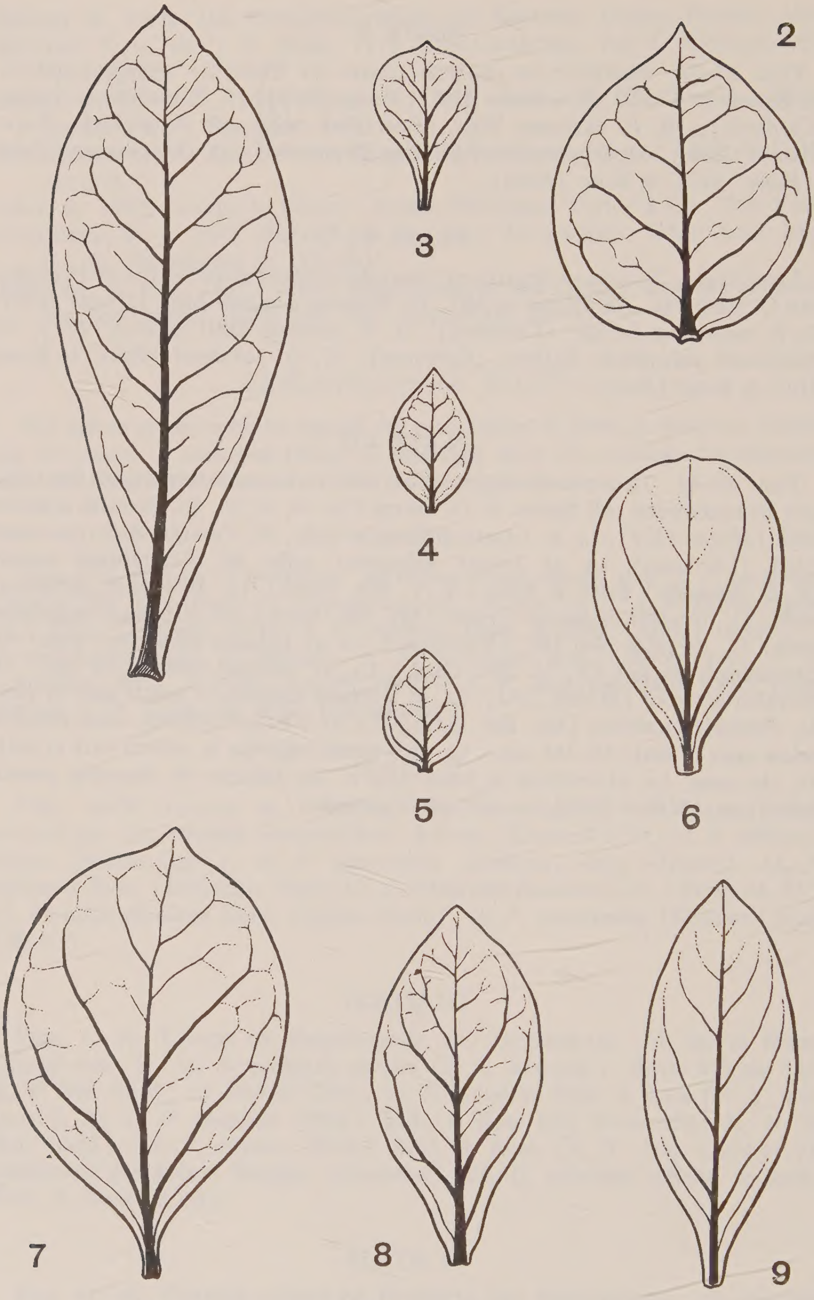
FIGS. 27–32. PORTIONS OF CLEARED LEAVES OF PERESKIA AND QUIABENTIA. All figures × 27. 27, *P. aculeata* Mill. [*Moran 7272*]; 28, *P. weberiana* Schum. [*Cárdenas*]; 29, *P. nicoyana* Web. [*Rodríguez 662*]; 30, *P. pititache* Karw. [Atkins Gard.]; 31, *Q. pereziensis* Backbg. [Cárdenas]; 32, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE VI

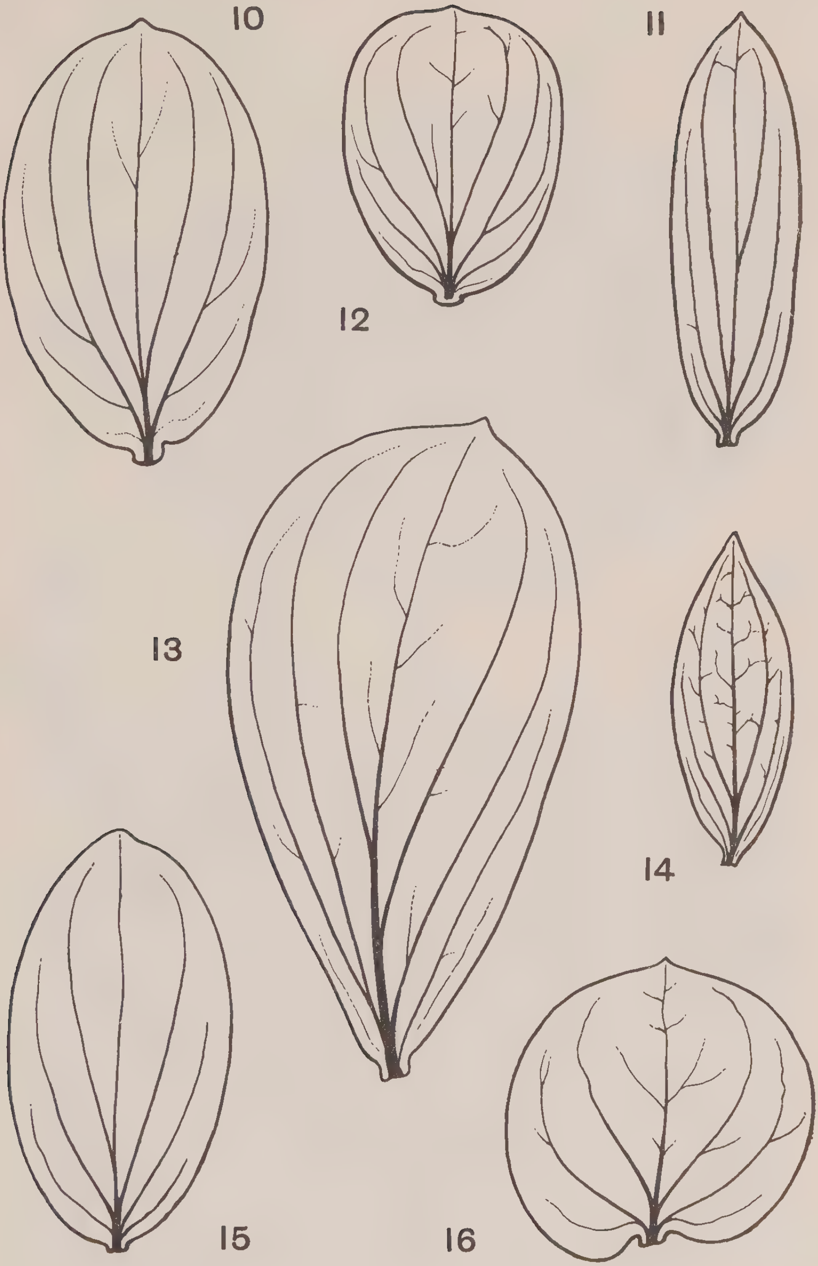
FIGS. 33–37. VASCULAR DETAILS OF VEINS AND VEINLETS IN LEAVES OF PERESKIA AND QUIABENTIA. All figures × 260. 33, *Pereskia aculeata* Mill. [*Moran 7272*]; 34, *P. weberiana* Schum. [*Cárdenas*]; 35, *P. aculeata* Mill. [*Moran 7272*]; 36, *Quiabentia pereziensis* Backbg. [*Cárdenas*]; 37, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE VII

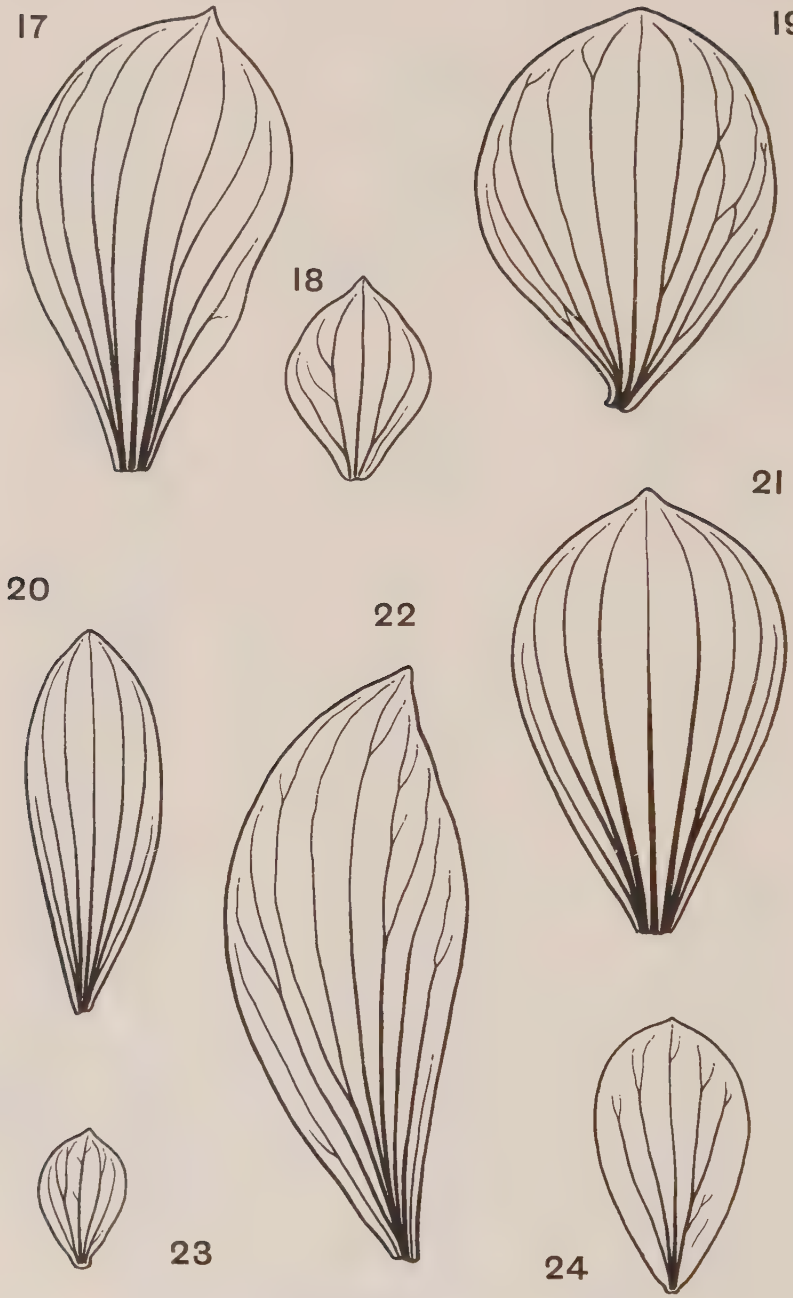
FIGS. 38–48. TRANSVERSE SECTIONS OF NODES AND OF MIDVEINS OF PERESKIA AND PERESKIOPSIS. All figures × 25, except FIG. 44, × 72. 38, *Pereskia aculeata* Mill. [*Moran 7272*]; t.s. at 2-trace unilacunar node; 39, *Pereskia diaz-romeroana* Card. [Cárdenas], t.s. at 2-trace unilacunar node; 40, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [N. Y. Bot. Gard.], t.s. at 4-trace unilacunar node; 41, *Pereskia sacharosa* Griseb. [Mo. Bot. Gard.], t.s. at 6-trace unilacunar node; 42, *Pereskia bleo* DC. [Rodríguez], t.s. at 10-trace unilacunar node; 43, *Pereskiopsis porteri* [N. Y. Bot. Gard.], t.s. of 2-strand midvein of leaf; 44, *Pereskia aculeata* [*Moran 7272*], t.s. of 2-strand midvein in apical part of leaf; 45, *Pereskia sacharosa* [Mo. Bot. Gard.], t.s. of 4-strand midvein some distance below apex of leaf; 46, *the same*, t.s. of 6-strand midvein in central part of leaf; 47, *the same*, t.s. of midvein in basal part of the lamina; 48, *Pereskia grandifolia* Haw. [*Moran 7270*], t.s. at base of petiole.



Bailey, Anatomy of Leaf-bearing Cactaceae, I



BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



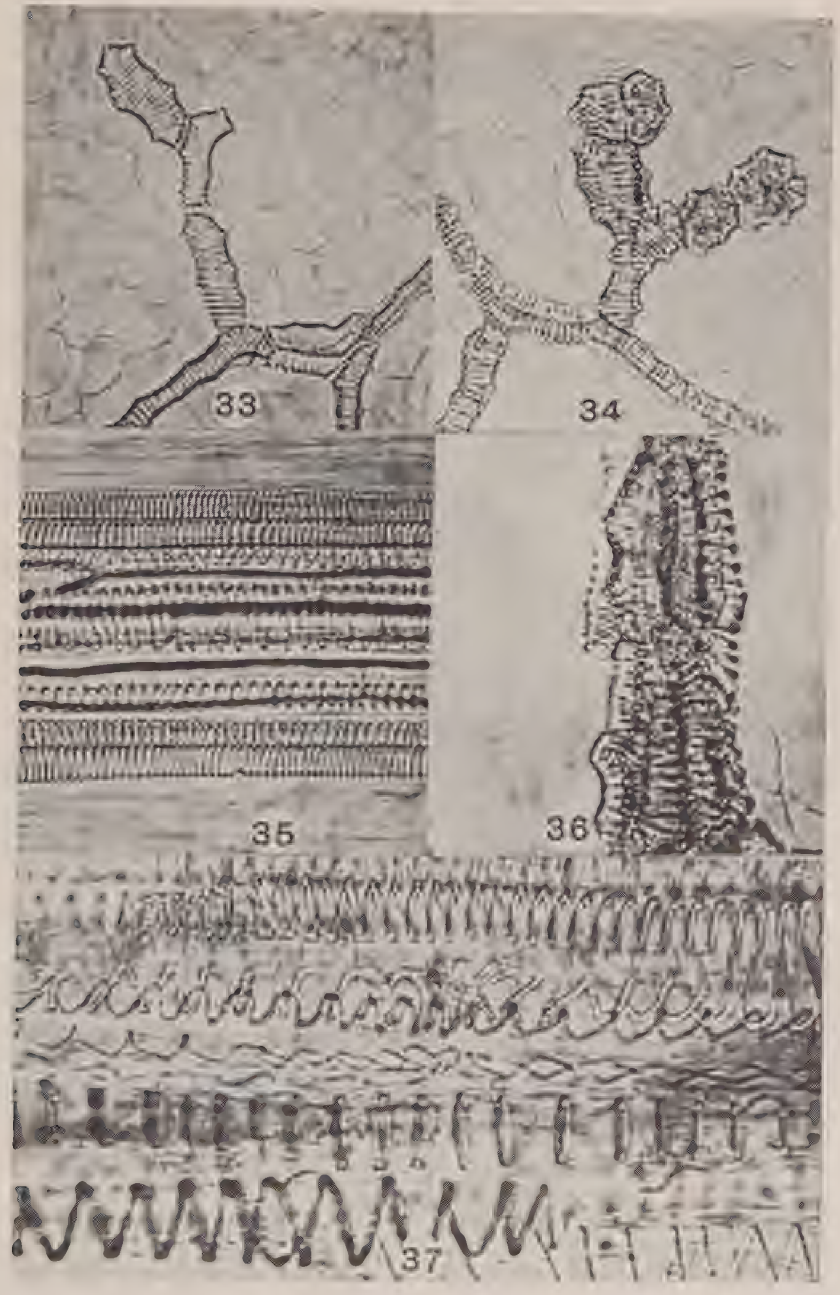
Bailey, Anatomy of Leaf-bearing Cactaceae, I

26

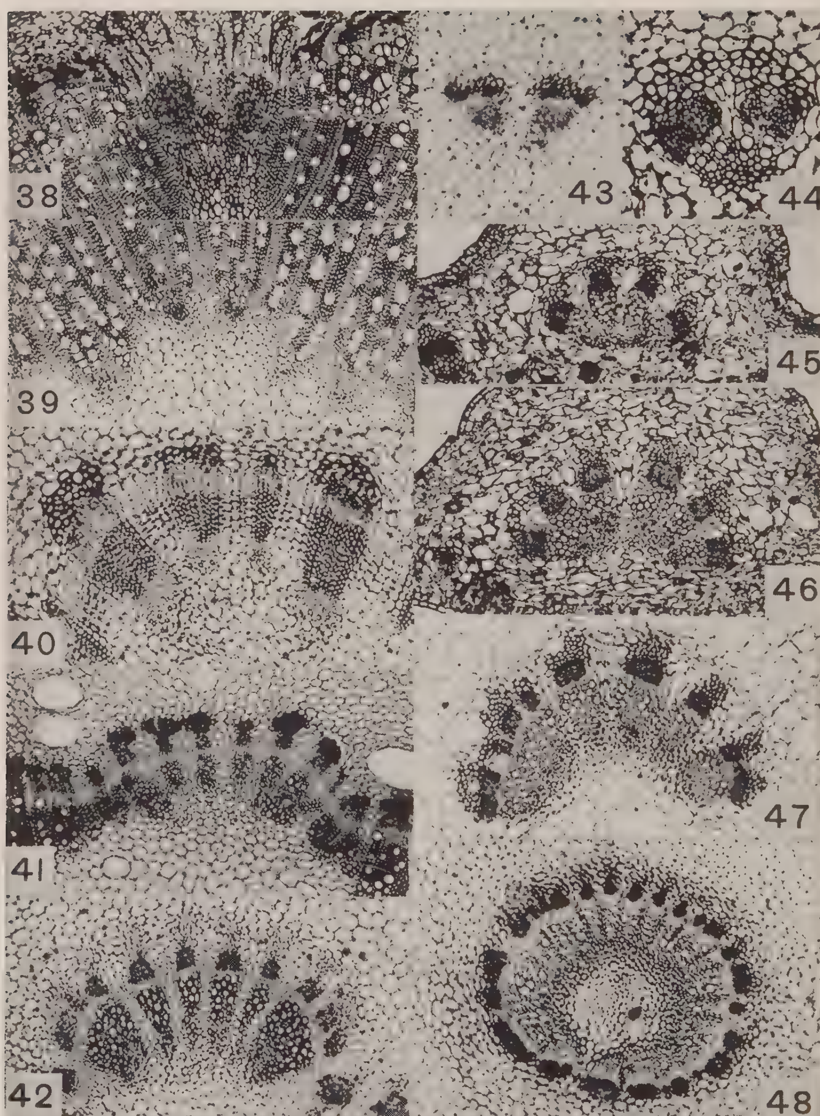
25

Bailey, Anatomy of Leaf-bearing Cactaceae, I

Bailey, Anatomy of Leaf-bearing Cactaceae, I



Bailey, Anatomy of Leaf-bearing Cactaceae, I



Bailey, Anatomy of Leaf-bearing Cactaceae, I

STUDIES IN THE GENUS COCCOLOBA, IX. A CRITIQUE ON THE SOUTH AMERICAN SPECIES *

RICHARD A. HOWARD

Coccoloba oblonga Lindau, Bot. Jahrb. **13**: 136. 1890.

This species was based on *Riedel 614* made near Ilheos, Bahia, Brazil. Lindau cited only the Leningrad specimen, although there is a large specimen in the Berlin herbarium. The species has been referred to the synonymy of *Coccoloba cruegeri* Lindau (*q.v.*). Lindau placed *C. cruegeri* in the section *Campderia* and *C. oblonga* in the section *Eucoccoloba*. I have indicated previously (Jour. Arnold Arb. **40**: 74. 1959) that there is no evidence that *C. cruegeri* belongs in *Campderia*.

Coccoloba obovata HBK. Nov. Gen. 2: 141. 1817; Howard, Jour. Arnold Arb. **40**: 209. 1959.

Coccoloba coriacea Willdenow ex Lindau, Bot. Jahrb. **13**: 194. 1890, not Sagra.
Coccoloba goudotiana Weddell, Ann. Sci. Nat. III. **13**: 260. 1850.

Coccoloba obovata was based on a Humboldt specimen collected in flower in June, 1805, at Honda, Colombia. A fine specimen in the Paris herbarium bears the most complete label and has been designated as the lectotype. *Coccoloba coriacea*, attributed to Willdenow, was published in synonymy by Lindau. The type of *C. goudotiana* (*Goudot s.n.* from San Luis, Colombia) is deposited in the Paris herbarium. It is clearly the same as *C. obovata*.

Most of the specimens seen have darkened in drying, the upper surface considerably darker than the lower leaf surface. In sterile condition this species is difficult to distinguish from comparable material of *Coccoloba coronata*, especially when it is represented by material from adventitious shoots. In general the ocreae of *C. coronata* are lighter in color and the petioles are shorter and stouter.

The species, with additional synonyms, is also known from Costa Rica and Panama.

Colombia. ANTIOQUIA: Medellín, *Toro 641* (NY); without specific location *Triana 981* (B). MAGDALENA: Cartagena, *Goudot s.n.* (P); San Andrés de la Sierra, *Pittier 1694* (GH). SANTA MARTA: Guamacito, *Record 34* (A, F, NY), *Espina 32* (F); Masinga, *Smith 421* (A, F, G, GH, NY, P), *422* (A, BR, P); Minca, *Espina & Giacometto A10* (F); Valparaíso, *Smith 1702*, in part (A, F, G, GH, NY, P). SANTANDER: Puerto Berrío, *Haught 1729* (NY, W). TOLIMA: Caucho, east

* Continued from volume XLI, p. 258.

of Prado, *Little 7171* (US); Hondo, *Humboldt s.n.* (P–lectotype, B), *Pennell 3555* (GH, NY); Mariquita, *Fernández 5637* (A). Without specific location: *Lehmann 1097* (A, F, GH, NY), *Goudot 0* (B), *1* (B). Dept. uncertain: Coyayoua, *Goudot s.n.* (P); San Luis, *Goudot s.n.* (P–type of *C. goudotiana*).

Coccoloba obtusifolia Jacquin, Enum. Pl. 19. 1760; Hist. Stirp. 114. 1763; Dugand, Caldasia **4**: 428. 1947.

Coccoloba billbergii Lindau, Bot. Jahrb. **13**: 219. 1890.

Jacquin's species was misplaced by Lindau and since that time, only Dugand, among the workers in South American floras, has included it. Jacquin stated the location of the species to be "Carthagenae in fruticosis & sylvaticis." Lindau placed the Jacquin name in the synonymy of *Coccoloba microstachya* Willd. under the variety *ovalifolia* Meisner. He did not cite Cartagena as a geographic location of the species or variety, but restricted *C. microstachya* to the northern Antilles. Meisner had previously recognized both *C. obtusifolia* and *C. microstachya*, but Lindau later noted that *C. obtusifolia* was published earlier than *C. microstachya* and so used the former name for the Antillean plant (Symb. Ant. **1**: 222. 1899). In his study of the flora of Colombia Dugand noted that *Coccoloba obtusifolia* was based on a plant from Cartagena and referred several collections to this name. He did not express clearly the geographic distribution of the species, but, from the references given, one infers Dugand's acceptance of the Antillean-Colombian range. However, *Coccoloba obtusifolia* Jacquin and "Coccoloba obtusifolia" of authors of West Indian floras are not the same species, as I have pointed out in a previous paper (Jour. Arnold Arb. **38**: 217. 1957). Lindau described the South American plant as *Coccoloba billbergii* and cited in synonymy "*Coccoloba obtusifolia* Meissn. (non Jacq.)," implying that he was creating a new species and that Meisner was in error.

Coccoloba obtusifolia is similar to and intergrades with several other species which are imperfectly known. The exact relationship to *C. peruviana*, *C. alagoensis*, *C. meissneriana*, *C. trianaei* and even *C. paraguariensis* cannot be determined at the present time. All but *C. meissneriana* were known to Lindau and considered in his monograph as belonging to section *Campderia*. Not one of them was known in fruit, however, and the placement of these species in *Campderia* was based on characteristics of the ocreolae and bracts. In his key to these species Lindau separated them on the basis of pubescence and leaf shape, both extremely variable characteristics. I am still handicapped by the lack of material, especially fruiting material of plants collected from the type locality of each species. I have considered uniting all of these species under *C. obtusifolia*, the oldest name for the complex, but have concluded that a wiser move at this time is to maintain all of the species, since it is impossible at present to distinguish them sufficiently to construct a key.

Coccoloba alagoensis was based on *Gardner 1389* from Alagôas in Brazil. In most of the following specimens assigned to this species the leaves

are shorter, thicker and more obtuse at the apex than those of specimens assigned to *C. peruviana*. Lindau assigned *Riedel 821* from Cuyaba, Matto Grosso, to *C. alagoensis*, thus extending the range beyond Alagôas. In his monograph he cited the Gardner collection as well as *Riedel 821* and reported specimens in the Barbey-Boissier, Leningrad and Vienna herbaria without specifying the locations of the individual collections. There is no material of Riedel in the Boissier collection and the Vienna collection has been destroyed, but the Leningrad herbarium has four full sheets of *Riedel 821* comprised of eleven branches. None has been annotated by Lindau. However, in the Berlin herbarium, not cited by Lindau but annotated by him, is one sheet of the Riedel collection which represents only the smallest leaf form of the eleven branches at Leningrad. I believe Lindau received this deceptive fragment and from it cited the material at Leningrad. *Riedel 821* is more similar to material of *C. peruviana* and should be so named. However, if Lindau's identification were followed, *C. peruviana* and *C. alagoensis* could not be distinguished.

The name *Coccoloba alagoensis* can be applied with certainty only to the type. With some hesitation I assign to it also the following Brazilian collections: Bahia, Jacobina, *Blanchet 2668* (B, NY, P), identified and cited by Lindau as *C. ovata*; Rio de Janeiro, *Glaziou 11443* (B), identified and cited by Lindau as *C. floribunda*. Minas Geraes: Serra do Caraca, *Glaziou 19767* (B, P), identified but not cited by Lindau as *C. ramosissima*. *Blanchet 2713*, from Jacobina, Bahia, is apparently a mixture, in part *C. ovata* (*q.v.*), the remainder assigned here.

Coccoloba peruviana is similar and intergrades in leaf size, shape and pubescence. In his key to the species, Lindau distinguished *C. alagoensis* by a glabrous rachis and *C. peruviana* by a rachis more or less puberulent. The problems associated with the accurate identification of *C. peruviana* will be discussed under that name.

Coccoloba meissneriana has leaves larger than those of *C. obtusifolia* but in the same range as *C. peruviana*. The pubescence is uniformly thick on the lower surface and present on the midrib and veins on the upper surface. The few specimens assigned to *C. meissneriana* can be related to typical specimens of *C. obtusifolia* through many intermediate specimens called *C. peruviana*. *Coccoloba trianaei* has leaves with longer acuminate tips and shorter, stouter and more pubescent petioles. *Coccoloba paraguariensis* is similar to *C. alagoensis*, being a smaller-leaved species with thicker, oblong leaf blades, shining when dry and conspicuously veined.

When a large number of these specimens are studied, it becomes obvious that these species are all related, though many questions arise which can be answered only by careful field examination not possible at this time. In his original description of *Coccoloba billbergii* Lindau cited *Billberg 204* and *204a*, with specimens in herbaria at Berlin and Stockholm. I have seen these specimens and find them to be an exact match of Jacquin's illustration. There are apparently no specimens in existence of Jacquin's species, so it must be typified by the illustration. When this is done, Dugand is correct in calling material from Colombia *C. obtusifolia*.

There is also some difficulty in typifying *Coccoloba billbergii* Lindau. Lindau cited two numbered collections, *Billberg 204*, and *204a*, and two herbaria, Berlin and Stockholm. There is only one unnumbered fragment at Berlin, although it bears a label identifying it as a Billberg collection, possibly in Billberg's hand, as well as Lindau's identification label, but the specimen's being small and unnumbered suggests that it may have been taken from one of the Stockholm collections. However, since Lindau saw this fragment in preparing his monograph, it seems proper to designate this specimen in the Berlin herbarium as the lectotype.

Jacquin's illustration is definitive on several points. In fruit, *Coccoloba obtusifolia* has relatively long, reflexed pedicels. The lobes of the fruiting perianth are free below the middle, and the leaf blades, while basically oblong, show some variation in size and shape. Dugand stated that the plants are shrubs, very branched and low, to 2 meters high (or rarely to 4 or 5 meters high) occurring very commonly in the dry thickets of the Colombian Caribbean seacoast. The specimens which Dugand cited are from the states of Atlántico, Bolívar, Guajira and Magdalena. I have seen the majority of them, in addition to the many others cited below, and find in them a great range of variation in size and shape. The final delimitation of this species will require comprehensive field study.

Colombia. ATLÁNTICO: Usiacurí, *Molina & Barkley 19 At 0.54* (US). BOLÍVAR: Cartagena, *Billberg s.n.* (B–lectotype of *C. billbergii*), *Bro. Heriberto 164* (GH, NY), *Schott 857* (NY); Lopopa, *Billberg 204* (S), *204a* (S); Soplaviento, *Killip & Smith 14587* (A, GH, NY). MAGDALENA: Barranquilla, *Bro. Elias 574* (A); Codazzi, *Haught 3711* (A), *3808* (BR, NY); Donjaca, *Record 70* (A, GH, NY, Y); La Paz, *Haught 2326* (A); Palmar de Varela, *Bro. Elias 765* (NY); Puerto Colombia, *Bro. Elias 386* (NY), *Bro. Paul 854* (A); Quemadito, *André 221* (K, NY); Santa Marta, *Goudot "Z"* (B, P), *Smith 412* (A, B, BR, NY, P), *792* (A, BR, NY, P); without definite locality, *André K-1592* (K, NY), *s.n.* (P). Locality uncertain: Isletas (Rio Nari ?Hari?) *André K-1593* (K, NY), Palanda, *André K-1591* (K, NY), Babahoya, *André K-1594* (K, NY). **Venezuela.** DEMOCRACIA: La Crisa, *Christ 41* (NY). ZULIA: San Martín on Río del Palmar, *Pittier 10519* (GH, NY).

Coccoloba ochreolata Weddell, Ann. Sci. Nat. III. 13: 259. 1850.

Coccoloba blanchetiana Weddell, Ann. Sci. Nat. III. **13**: 257. 1850.
Coccoloba bracteolosa Meisner, Fl. Bras. **5**(1): 30. 1855.

Meisner was the first monographer to suggest that the two species described by Weddell were identical and, although there is some question whether Meisner saw all of the material that Weddell studied, Lindau (Bot. Jahrb. 13: 169. 1890) accepted his decision, citing the complete collections of Blanchet. I have seen the types and duplicates of both Weddell species and agree that they are to be considered identical.

Meisner also described *Coccoloba bracteolosa*, based on Martius collections from the state of Bahia. These flowering specimens have slightly immature leaves. In an earlier paper (Jour. Arnold Arb. **40**: 211. 1959)

the species was referred to the synonymy of *C. parimensis* with the qualification that additional material might prove it to be better placed with *C. ochreolata*. I have now seen sufficient material to refer *C. bracteolosa* to the synonymy of *C. ochreolata* without hesitation. Lindau distinguished these species in the key in his monograph on the shape of the leaf base, narrowed in *C. bracteolosa* and rounded or cordate in *C. ochreolata*. He treated the species successively in the text, but I am unable to find any characteristics in the descriptions or in the specimens cited which would sustain a separation.

Mason & Harvey 6700, from Panama, previously cited by Lundell (Contr. Univ. Mich. Herb. 6: 9. 1941) as *Coccoloba bracteolosa* and referred by me to *C. parimensis* is correctly placed there. Likewise a Martius collection from Pará in the Brussels herbarium cited by Lindau as *C. bracteolosa* is also referred to *C. parimensis*.

Coccoloba ochreolata is very similar to *C. ilheensis*, especially at the time of flowering when the leaves are slightly immature. The latter species is not known in fruit. Additional collections are needed to determine the correct relationship of these two species.

Brazil. BAHIA: Jacobina, *Blanchet 3394* (B, LE, P), *3561* (P–holotype of *C. blanchetiana*, BR, LE, NY); Joazeiro, on Rio San Francisco, *Martius s.n.* (M–holotype of *C. bracteolosa*); without specific locality, *Blanchet 3410* (P–holotype), *3410B* (LE, NY, P), *Bondar s.n.* (F), *Clausen 46* (P). ESPÍRITO SANTO: between Campos & Victoria, *Sellow 405* (B). RIO DE JANEIRO: Maná, *Glaziou 18428* (P); Therezopolis, Serra dos Orgãos, *Glaziou 3088* (BR, P).

Coccoloba orbicularis Loddiges Cat. ex Loudon, Hort. Brit. 159. 1830.

In a list of stove plants with accompanying symbols to characterize the horticultural details of the plants Loudon cited this name which he attributed to the catalogue of the Loddiges Nursery at Hackney, near London, where he said the plant was introduced from South America in 1825. The only two Loddiges Catalogues available to me are those of the years 1820 and 1823, in which the name is not used. Later, in a list of excluded species Lindau (Bot. Jahrb. 13: 220. 1890) made the following notation: "*C. orbicularis* Lodd. = *Mühlenbeckia* (?) *orbicularis* Lodd." Jackson (Index Kewensis 1: 573. 1895) listed *Coccoloba orbicularis* Lodd. Cat. ex Loud. Hort. Brit. in italics as an excluded species, but referred it without hesitation to *Muehlenbeckia orbicularis*. However, the name "*Muehlenbeckia orbicularis*" is not listed in Index Kewensis under that genus, nor can I find it in any existing monograph or flora.

Loudon's symbolic description can scarcely be considered valid publication and thus the epithet should be considered a *nomen nudum*. Very probably the plant in question is *Coccoloba caracasana* described by Meisner in 1856.

Coccoloba ovata Bentham in Hooker, London Jour. Bot. 4: 627. 1845.

Coccoloba ovata var. *major* Meisner, Fl. Bras. 5(1): 31. 1855.

Coccoloba ovata var. *minor* Meisner, *ibid.*
Coccoloba ovata var. *lanceolata* Meisner, *ibid.*
Coccoloba moritzii var. *opaca* Meisner, Fl. Bras. **5**(1): 28. 1855.
Coccoloba moritzii var. *lucida* Meisner *ibid.*
Campderia gracilis Meisner, Fl. Bras. **5**(1): 26, *pls. 6.* 1855.
Coccoloba nigra Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Fl. Jamaica **3**: 120. 1914; Howard, Jour. Arnold Arb. **38**: 106. 1957.

The current delimitation of *Coccoloba ovata* is not a satisfactory one. Only deliberate effort on the part of some collector in the area will obtain the necessary material to allow an understanding of the sexual condition, the habit and leaf variation and the true nature and development of the fruit.

As described by Bentham *Coccoloba ovata* was based on *Schomburgk 531* and *893* from the first Schomburgk expedition. *Schomburgk 531* (K) is designated as the lectotype. In the discussion Bentham stated, "This species appears to have an extensive range, if specimens which I have from various parts of tropical Brazil and from the West Indies are, as they appear to be, referable to it. It agrees in many respects with the characters given of *C. obtusifolia*, Jacq., but the leaves, though variable in form, are never so narrow as those described by Jacquin; nor does the inflorescence agree at all with that attributed to the *C. microstachya*, Willd., which is said to differ chiefly from *C. obtusifolia*, by its broad leaves." Bentham does not cite any specimens from the West Indies and *C. ovata* is not known from there. *Coccoloba obtusifolia* Jacq. and *C. microstachya* Willd. have been misinterpreted and considered synonymous by some authors. In reality *C. obtusifolia*, though a variable species, is from Venezuela while *C. microstachya*, quite distinct from it, has its center of distribution in Puerto Rico and is not known from South America. I can agree with Bentham that *C. ovata* is not at all related to *C. obtusifolia* or to *C. microstachya.*

Bentham indicated the variability in leaf shape and size in the original Latin description and in his discussion. Meisner placed further emphasis on this variability when he described *C. ovata* var. *major*, citing specimens including *Schomburgk 893* and varieties *minor* and *lanceolata* citing *Schomburgk 531*, in part, among the specimens assigned to each variety. I have not seen specimens bearing Meisner's annotation, but the specimens of *Schomburgk 531* and *893* which I have seen I believe are easily accommodated in one species. The specimens appear to come from scrambling branches, although Bentham reported the plant to be a shrub.

Meisner also described *Coccoloba moritzii* in *Flora Brasiliensis*, recognizing two varieties as comprising the species. He cited only a collection from Colombia, *Moritz 550*, as representing *C. moritzii* var. *opaca* and a Schomburgk collection without number from British Guiana for *C. moritzii* var. *lucida*. The name *C. moritzii* was attributed to Klotzsch, who apparently wrote "Coccoloba moritziana Kl." on a specimen in the Berlin herbarium. This specimen cannot be located. A Schomburgk speci-

men without number bearing the name "Coccoloba moritzii Kl. β lucida Meisn." is in the collections of the Berlin herbarium. I find this specimen comparable in all characters to other material of *Schomburgk 531* and believe the original collector's data were lost from this specimen. Lindau has placed *C. moritzii* and its varieties in the synonymy of *C. ovata*, and I believe this to be the correct handling of Meisner's species.

Bentham did not have the fruit when he described *Coccoloba ovata*, nor did Meisner when he considered the species in *Flora Brasiliensis* and the *Prodromus*. Lindau, however, did describe the fruit in his monograph (Bot. Jahrb. 13: 216, *fig. 54.* 1890) as follows: "Fructus ovoideus, circa 15 mm. longus, 7 mm. diametro, lobis accrescentibus coronatus, demum pericarpii carne evanida nervis carinalibus nervulisque persistentibus, ruber, facile deciduus." I have not seen all of the collections cited by Lindau, but the fruit which he described for *C. ovata* is present in packets on *Poeppig 2617* and *2634*, as well as on some of the recent collections cited below. The fruit is most unusual and is certainly atypical of even a broad concept of the genus. It is possible that after careful field study of *Coccoloba ovata* a new genus may be created to accommodate this species.

As presently known, *Coccoloba ovata* is a tree (possibly with scrambling branches), a shrub, or a vine. The leaves are mainly ovate but vary from lanceolate-ovate to oblong, narrowed or obtusely cordate at the base and obtuse, acute, or acuminate at the apex. The young branches, ocreae and petioles are crispose-pilose when young, becoming glabrate. The leaves are of firm texture and generally shiny on both sides when dry. The inflorescence ranges in length from 4 to 25 cm. and the flower clusters may be closely arranged or clearly distinct. The principal bract, subtending the flower, is generally black in color, ovate in outline but commonly long-attenuate at the apex. The ocreolae are membranaceous and conspicuous. Functionally staminate flowers tend to be numerous (ca. 10), functionally pistillate flowers (on other inflorescences) fewer (2–6). No specimens are available with both flowers and fruit. The pistillate flowers appear to be typical of *Coccoloba*. In fruiting condition the peduncles elongate, becoming 1–3 mm. long. In an occasional specimen the ocreola is fused to the peduncle. The fruiting perianth is large, becoming 15–17 mm. long. The hypanthium extends to the middle of the elongated achene and the perianth lobes extend well beyond the apex of the achene. The outer two, rarely three, perianth lobes are sharply keeled and appear to have been fleshy. The two inner perianth lobes scarcely exceed the apex of the achene and are flat. The perianth lobes are not tightly imbricate in the fashion found in *C. venosa* or Lindau's section *Campderia*, nor are they coronate, as Lindau stated, in the fashion of *Coccoloba swartzii*. In superficial aspect the fruiting perianth appears to be intermediate between *Symmeria* and *Triplaris*, or a fleshy elaboration of the imbricate-lobed type of the Campderia section. A number of the characteristics given above suggest that a special genus is required for *Coccoloba ovata*, but the lack of adequate field knowledge of this species prevents me from creating one at this time.

Campderia gracilis Meisner was described and illustrated in the *Flora Brasiliensis*. The original description refers to only one collection, *Spruce s.n.*, from Barra on the Rio Negro in Brazil. In the *Prodromus* Meisner reported specimens in Delessert and Munich herbaria. I have seen both of these specimens and six additional ones. No single specimen compares exactly with the illustration given in *Flora Brasiliensis*, and, consequently, I conclude that certain artistic liberties were taken. The original detailed sketch of the flower and fruit which appears on the *Flora Brasiliensis* plate is attached to a sheet in the Munich herbarium. This should be considered the lectotype. No achenes have been found on any specimens of this Spruce collection and I wonder where Meisner obtained the material for the illustration. Lindau assigned *Campderia gracilis* to the synonymy of *Coccoloba ovata*. If Meisner's illustration of the fruit of *Campderia gracilis* is correct and if, in following Lindau I have interpreted the fruit correctly, the species cannot be accommodated in *Coccoloba ovata*. However, if Meisner's illustration of the fruit is in error, as it appears to be on the basis of material I have seen, then *Campderia gracilis* must be considered as known only from flowering specimens and may well be placed correctly in the synonymy of *Coccoloba ovata*.

Passarge and Selwyn 491, made on the German Caura Expedition into the Guiana of Venezuela in 1901–1902, has been annotated with an unpublished name by Gross, who studied this specimen in the preparation of a treatment for *Pflanzenreich*. The majority of the new names he used appear to be unpublished. The present collection in the Berlin herbarium consists of two detached leaves and five detached inflorescences. The leaves are oblong-lanceolate and the inflorescences are from pistillate plants. The material is included in the broad concept of *Coccoloba ovata* which I am using.

Blanchet 2713 apparently is a mixture. A specimen so numbered in the Prodromus herbarium bears the label "villa de Barra" and belongs in this species, but a specimen carrying the same number, originally from Meisner's herbarium but now in the herbarium of the New York Botanical Garden, gives the location as "Serra de Jacobina Prov. Bahia" and is *Coccoloba alagoensis*.

Brazil. AMAZONAS: Barra, *Spruce 958* (M-lectotype of *Campderia gracilis*, B, G, GH, LE, P), *Blanchet 2713* in part (G); Manaos, *Ducke 348* (A, F, K, NY, US); Rio Coary, *Martius s.n.* (M); *Rio Negro, Spruce s.n.* (M); Rio Yapurá, *Martius s.n.* (M); without locality, *Poeppig 2617* (LE). BAHIA: Borba, *Riedel 1366* (LE, P). PARÁ: Bôa Vista on the Tapajoz River, *Dahlgren & Sella 61* (B, F); lower Cupari River, *Krukoff 1206* (A, NY, P). State unknown: Ega, *Poeppig 2634* (B, G, LE). **British Guiana.** DEMERARA: Matope Falls of the Cuyuni River, *Forest Dept. F–3380* (NY), *3382* (NY). Without locality: *Jenmann 1074* (P); *Schomburgk 531* (K–lectotype, BM, P), *893* (NY, P), *s.n.* (B). **Colombia.** VAUPÉS: Río Guaviare, *Molina & Barkley 215* (US); Río Inírida, *Fernández 2279* (A, US); Río Papunáua, *Fernández 2038* (A, US). **Venezuela.** AMAZONAS: Río Orinoco near mouth of Río Atabapo, *Wurdack & Adderley 42722* (A, NY). APURE: Río Cinaruco between mouth and Las Galeras de Cinaruco, *Wurdack*

& Monachino 41361 (A, NY). BOLÍVAR: Caño Coroso between Lago Coroso and Río Orinoco, *Wurdack & Monachino 41192* (A, NY); Ciudad Bolívar, *Pittier 13951* (US); Llanos de l'Aprure, *Geay s.n.* (P); Río Orinoco between Río Paragua and Río Horeda, *Wurdack & Monachino 39878* (A, NY); Río Paragua, *Cardona 1088* (F, NY, US); without specific locality, *Passarge & Selwyn 491* (B). Country undetermined: Upper Orinoco, *Gaillard 198* (P).

Coccolobis padifolia Rusby, Mem. N.Y. Bot. Gard. 7: 235. 1927.

The type of this species, *Mulford Biological Expedition 848* (NY) from Rurrenabaque, Bolivia, has been compared with the type of *Coccoloba longipes* S. Moore from the Matto Grosso of Brazil. The species are the same and *C. padifolia* is referred to synonymy.

Coccoloba padiformis Meisner, DC. Prodr. **14**: 166. 1856; Howard, Jour. Arnold Arb. **40**: 210. 1959.

Coccoloba sphaerococca Lindau, Bot. Jahrb. **13**: 185. 1890.

It has been pointed out previously that *Coccoloba padiformis* and *C. densifrons* are very similar. For the present *C. densifrons* is distinguished by its larger and heavier leaves which are generally broadest above the middle, by the conspicuous, arcuate, impressed primary venation and by the stouter and longer inflorescence axis.

Coccoloba padiformis is more similar to *C. sphaerococca.* Lindau described a puberulent inflorescence rachis for *C. padiformis* to distinguish it from *C. sphaerococca* which is supposed to have a glabrous one, but the type specimen of *C. sphaerococca* is an old fruiting specimen with some pubescence present in protected spots on the rachis, while the type specimen of *C. padiformis* is a staminate flowering branch, so Lindau's distinction does not seem reliable. *Coccoloba sphaerococca* was based on material collected at Tarapoto, Peru; *C. padiformis* is typified by a specimen from Caracas, Venezuela. Macbride assigned additional collections (*Killip & Smith 29027*, *27958* and *Williams 3805*) to *C. sphaerococca,* but I believe these specimens belong instead to *C. nutans.*

Lindau (Bot. Jahrb. 13: 201. 1890) broadened the original concept of *Coccoloba candolleana* to include material collected by Goudot in Colombia (*Goudot 4*) which is clearly to be referred to *C. padiformis.*

An additional species from Costa Rica has been previously referred to synonymy here (Howard, *loc. cit.*) and material has also been seen from Panama.

Colombia. CAUCA: Vallée du Cauca, *Triana 975* (P). MAGDALENA: Mariquita, Piedras du Magdalena, *Triana 976* (P); Santa Marta, *Smith 1696a* (A, NY), *Goudot 4* (B, P). **Peru.** SAN MARTÍN: Tarapoto, *Spruce s.n.* (K-holotype of *C. sphaerococca*). **Venezuela.** FEDERAL DISTRICT: Caracas, *Moritz 377* (M–holotype, G, LE, NY). MIRANDA: Pice de Naiguatá, *Pittier 6190* (NY). ZULIA: Maracaibo Lake at Río Limón, *Curran & Haman 796* (A, GH).

Coccoloba paniculata Meisner, Fl. Bras. 5(1): 43. 1855.

The typification of *Coccoloba paniculata* Meisner would be a difficult taxonomic problem, since Meisner included in the original citation the type of *C. polystachya* Weddell. Fortunately a solution is not necessary, since *C. mollis* Casaretto represents the older, legitimate name. A full discussion of the types and relationships is given under *C. mollis.*

Coccoloba paraensis Meisner, Fl. Bras. 5(1): 38. 1855.

This species was based on *Spruce 957*, from Manáos, Brazil, and a Martius collection from the state of Pará. I indicated in an earlier paper (Jour. Arnold Arb. **40**: 211. 1959) my belief that this species is properly placed in the synonymy of *Coccoloba parimensis* Bentham.

Coccoloba paraguariensis Lindau, Bot. Jahrb. **13**: 218. 1890.

Coccoloba microphylla Morong in Morong & Britton, Enum. Pl. 212. 1892; Ann. N.Y. Acad. **7**: 213. 1893, not Griseb. 1866.
Coccoloba morongii Hassler, Repert. Sp. Nov. **14**: 162. 1915.

In the original description Lindau cited the single collection *Balansa 2060* and only the specimen in the herbarium at Göttingen. It is important to note that the description and the specimen agree. Unfortunately this collection has proved to be a mixed one and specimens which I have seen bearing this number are all to be referred to *Coccoloba spinescens*, with the sole exception of the holotype at Göttingen. The misinterpretation of *C. paraguariensis* by recent workers has led to the confusion evident in the synonymy given here and under *C. spinescens.*

Coccoloba microphylla Morong was based on *Morong 899* gathered along the Pilcomayo River in Paraguay. The epithet is a later homonym of *C. microphylla* Grisebach, as was recognized by Hassler, who renamed the species *C. morongii.*

Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 251. 1959) have referred *Coccoloba paraguariensis* to the synonymy of *C. alagoensis* Weddell and have accepted *C. morongii* as a distinct species. I cannot agree with this treatment.

Coccoloba corrientina Rojas (Bull. Geogr. Bot. **28**: 162. 1918) has been treated by Buchinger and Sanchez, *loc. cit.*, as an "especie dudosa" but with the suggestion of similarities to "C. morongii." Rojas' description is brief and generalized and no specimens are cited. Dr. Buchinger wrote that no material attributable to this species from the Rojas collection could be found. It is my belief that *C. corrientina* Rojas is properly placed in the synonymy of *C. paraguariensis.*

Argentina. CHACO: Fontana, *Meyer 2.276* (A). CORRIENTES: Puenta Pesca, *Ibarrola 251* (W). FORMOSA: *Jórgensen 1985* (GH, US), *Rojas 11557* (A). **Paraguay.** Along the Pilcomayo River, *Morong 899* (NY–type of *C. microphylla*, GH), *Rojas 196* (GH), *196*a (B, GH, K); escarpments along the Río Paraguay, *Balansa 2060* in part (GOET–holotype).

Coccoloba parimensis Bentham in Hooker, London Jour. Bot. **4**: 626. 1845; Howard, Jour. Arnold Arb. **40**: 211. 1959.

Coccoloba parimensis var. *schomburgkii* Meisner, Fl. Bras. **5**(1): 35. 1855.
Coccoloba excelsa var. *glabra* Lindau, Bot. Jahrb. **13**: 171. 1890.
Coccoloba paraensis Meisner, Fl. Bras. **5**(1): 38. 1855.

A full discussion of *Coccoloba parimensis*, its variations and relationships is given in the earlier paper cited above, where additional specimens from Panama are referred to this species.

Brazil. AMAZONAS: Airão, Rio Negro, *Murca Pires 243* (NY, US); Barra, *Spruce s.n.* (B, GH, LE); Ega, *Poeppig 2670* (LE); Humaytá near Livramento, *Krukoff 6606* (A, BR, LE, NY); Manáos, *Ducke 1289* (A, F, NY, US); Panuré, Rio Uapes, *Spruce 2732* (B, G); Paraná, de São José de Arirahá, *Baldwin 3299* (US). PARÁ: Eastern region, *Martius s.n.* (BR); Iquapémirim, *Martius s.n.* (M). **British Guiana.** Barima River, Northwest District, *De La Cruz 3359* (GH, NY, US); east of Atkinson Field, *Irwin 241* (US); Malali, Demerara River, *De La Cruz 2668* (GH, NY, US). **French Guiana.** Cayenne, *Martin s.n.* (K); Savane de Charvin, near St. Laurent, *Cowan 38874* (NY). **Peru.** LORETO: Mishuhuaca near Iquitos, *Klug 1592* (A, F, NY); Yurimaguas, *Llewelyn Williams 4528* (F). **Venezuela.** AMAZONAS: Caño Avatapure, *B. & C. Maguire 35526* (A, NY); Maroa, Río Guainia, *Llewelyn Williams 14259* (F, US); Pimichín, *Llewelyn Williams 14188* (F); Pto. Ayacucho, Río Orinoco, *Curran 1813* (NY). BOLÍVAR: Alto Cuyuni, Río Chicanang, *Cardona 2767* (NY).

Coccoloba parvifolia Schott in Sprengel, Syst. Veg. **4**(2): 405. 1827; Lindau, Bot. Jahrb. **13**: 175. 1890, not Poiret (1804).

Lindau accepted the epithet *Coccoloba parvifolia* Schott in his monograph of the genus. He referred the older name, *C. parvifolia* Poiret (Lam. Encycl. **6**: 64. 1804), to the synonymy of *C. microstachya* var. *ovalifolia* Meisner. Under the present rules of nomenclature, *C. parvifolia* is preoccupied and *C. parvifolia* Schott is a later homonym. The correct name for this species is therefore *C. rigida* Meisner.

The original description of *Coccoloba parvifolia* Schott is brief and no specimens are cited. A specimen in the Berlin herbarium obtained with the Kurt Sprengel herbarium is presumed to be the holotype. This herbarium was acquired after 1890 and the specimen in question was not annotated (and perhaps not seen) by Lindau. The Berlin herbarium does contain four collections (*Schott 5538*, *Riedel 683*, *Schenck 3939*, and *St. Hilaire 138*) which Lindau saw and annotated. The Sprengel herbarium specimen without number matches *St. Hilaire 138*.

Coccoloba peltata Schott in Sprengel, Syst. Veg. **4**(2): 405. 1827; Lindau, Bot. Jahrb. **13**: 181. 1890.

Coccoloba peltigera Meisner, Fl. Bras. **5**(1): 39, *pl. 17*. 1855.
Coccoloba nymphaeifolia Schenk in Zittel, Handb. Palaeont. **2**: 491. 1887, nomen nudum.
Coccoloba erecta Glaziou, Bull. Soc. Bot. Fr. IV. **11**(Mem. 3f): 572. 1911, in part.

Coccoloba peltata is listed in Sprengel's *Systema* with a very short description and no specimens are cited. The specimen from the Sprengel herbarium now at Berlin consists of a single detached leaf, but this was collected by Schott. It is not annotated by Lindau and perhaps was not seen by him. Nevertheless, this specimen must be considered the holotype of *C. peltata*.

Meisner recognized *Coccoloba peltata* but did not see any material and only repeated the original description. At the same time Meisner described *C. peltigera*, recognizing it as only slightly different from the inadequately described *C. peltata*. Lindau reduced *C. peltigera* to synonymy under *C. peltata* Schott, and I believe he was correct in doing so.

For *Coccoloba peltigera* Meisner cited *Martius 238* and *Poeppig 2670*, placing in synonymy the manuscript name "Coccoloba scandens Poeppig" for the latter specimen. The illustration given in *Flora Brasiliensis* was compiled from two specimens of *Martius 238*, now in the Munich herbarium. No type was selected, but it seems desirable to designate *Martius 238* as the lectotype of *C. peltigera*. Martius did not give the location of the Poeppig specimen, but Lindau referred to the same manuscript name on a specimen in the Vienna herbarium. This collection at Vienna was lost during World War II, but a specimen of the same number without the manuscript name is in the Leningrad herbarium. This specimen is to be referred to *C. parimensis*.

I have already discussed the epithet *Coccoloba nymphaeifolia* (*q.v.*) which is a *nomen nudum*. I have also previously indicated that *C. erecta* Glaziou must be considered a *nomen nudum*. However, in the place of publication Glaziou cited *Glaziou 14220* for *C. erecta* and *Glaziou 14219* for *C. schwackeana*. Unfortunately both of these collections are mixed and specimens labeled *Glaziou 14219* may be either *C. schwackeana* or the present species.

Coccoloba peltata is not well represented in herbaria but appears to be characterized, as originally described, by having leaves with long petioles and blades which are usually, but not always, peltate. In petiole length it compares with *C. tiliacea* from Argentina, a species which also has peltate or non-peltate leaves. *Coccoloba tiliacea* differs in having pedicellate flowers and fruits on lax or more tenuous rachises. The specimens cited below are mostly from lianas or "ropelike" branches. The species is not known in fruit. Many of the specimens give the impression of representing abnormal growth forms. Leaf blades vary in size and shape, in many cases approaching the thick leaf types of *C. marginata*. The inflorescence has been found divided and is apparently fasciated in *Glaziou 14219* (LE). A study of this species in the field may reveal it to be only a teratological or abnormal form of some other species. For example, it is possible that some of the material I have called *C. marginata*, particularly the Salzmann collections from Bahia labeled "Coccoloba pendula" or "Coccoloba nitida var. cordata" in herbaria, may be the normal expression of *C. peltata*. At present the distinctions between *C. marginata* and *C. peltata* are not clear.

Brazil. Rio de Janeiro: Copacabana, *Nadeaud s.n.* (p); Corcovado, *Beyrich s.n.* (p); São Christovão, *Glaziou 14219* in part (le, p); without specific location, *Glaziou 144* (br, p), *Martius 238* (m–holotype of *C. peltigera*). Without location: *Schott s.n.* (b–lectotype of *C. peltata*), *Clausen 57* (p). **Cultivated material:** *Herb. Fischer* (le), *Herb. Lips.* (b).

Coccoloba pendula Salzmann ex Lindau, Bot. Jahrb. 13: 180. 1890.

This epithet was invalidly published by Lindau in the synonymy of his "Coccoloba nitida." I have restricted *Coccoloba nitida* HBK., both in definition and distribution, and cannot include the Salzmann specimens cited by Lindau. These specimens from Bahia, Brazil, are all without numbers but bear different annotations; e.g., "C. pendula," "C. nitida var. cordata" or "C. tenuifolia Lam.," and have been seen in many European herbaria. All should be referred to *C. marginata*, with the possibility that they may represent normal growth forms of *C. peltata*.

Coccoloba persicaria Weddell, Ann. Sci. Nat. III. 13: 256. 1850.

This species is similar to *Coccoloba gracilis*, *C. obtusifolia*, and *C. spinescens*. At present it is distinguished by the broader leaves, shorter petioles and more pubescent branches and foliage. The holotype is in the Paris herbarium and a fragment of the holotype is in Berlin.

A second collection from Bolivia, *Kuntze s.n.*, should be assigned here. In the preparation for a treatment of this genus for Pflanzenreich, Gross assigned new names to many collections. Some of these names were published in short notes, often in obscure publications. This particular collection bears a specific name honoring Otto Kuntze, and, if it has been published, it should be assigned to the synonymy of *C. persicaria*.

Bolivia. Tunari, *Kuntze s.n.* (b, ny); Yungas, *Weddell 4257* (p–holotype, b).

Coccoloba peruviana Lindau, Bot. Jahrb. 13: 213. 1890.

Lindau described this species and cited two collections, *Ruiz & Pavon 229* and *D'Orbigny 571*, in the original publication. Macbride (Field Mus. Pub. Bot. 13: 461. 1937) also considered the species, adding three collections, *Llewelyn Williams 2482*, *6847* and *6852*, and designated as the type *Ruiz & Pavon 229*. No location was given for the lectotype, but a photograph of the Ruiz and Pavon specimen in the Berlin herbarium is deposited at the Chicago National History Museum. The photograph bears the general label, "Types of the Berlin Herbarium," and, since Lindau annotated the sheet, it seems proper to accept the fragments, a small sterile shoot, a detached inflorescence and a single leaf, as the holotype. Additional and better specimens of this collection have been seen in the herbaria at Geneva. Another specimen, presumably of the same collection but without number, was obtained by the Chicago Natural History Museum recently from the Ruiz & Pavon collections at Madrid. I have seen *D'Orbigny 571* from Bolivia in the herbarium at Paris and

there is no question that the Ruiz and Pavon and D'Orbigny collections, both of which are in flower, represent the same species. I have also seen the Williams collections cited by Macbride. *Williams 6847* has very few flowers left on one of several inflorescences present on the sheet. *Williams 6852* is comparable in all respects except for a number of immature fruit found in a packet. Both specimens show smaller leaves of thinner texture than do the specimens first cited by Lindau. *Williams 2482* has leaves comparable to the Ruiz & Pavon type, but attached to the sheet is a packet containing fruits which are different from those of *Williams 6852*, although similar to those of *C. ovata* which I find difficult to accommodate in the genus. In mature condition these fruits have a jet-black, triangular achene, one-third to one-half the length of the membranaceous perianth lobes, which are free to the base in fruit and expanded, imbricate, heavily veined and membranaceous. In contrast to these are the fruits of *Ule 9349* made along the Rio Acre. These fruits are typical of *C. obtusifolia*, with tightly appressed perianth lobes free to the base and scarcely exceeding the smaller, tan-colored achenes. The leaves and inflorescences of the Ule collection compare favorably with the Ruiz and Pavon collection. The Riedel collection from Cuyaba has fruits comparable to *Ule 9349*. I am unable to determine from the material at hand which fruit type belongs with *C. peruviana* as typified by *Ruiz & Pavon 229*. Until field studies can be made or more adequate collections are available which will show fruit variation within a population, as well as staminate and pistillate inflorescences, *C. peruviana* will not be clearly defined.

Bolivia. Without specific location, *D'Orbigny 571* (P). **Brazil.** AMAZONAS: Rio Acre, *Ule 9349* (G, K, NY, US). MATTO GROSSO: Cuyabá, *Riedel 821* (B, LE, P). **Peru.** LORETO: Middle Ucayali, *Tesmann 3226* (F, NY), *3231* (NY). SAN MARTÍN: Juan Guerra, *Williams 6847* (F), *6852* (F). Without specific location: *Ruiz & Pavon 229* (B–lectotype, G), *s.n.* (F).

Coccoloba pichuna Huber, Bol. Mus. Goeldi **5**: 342. 1909.

This species is based on *Ducke 4866*, from Obidos, Pará, Brazil. I have seen a duplicate in the British Museum. The species is to be referred to the synonymy of *Coccoloba densifrons* Martius ex Meisner.

Coccoloba pipericarpa Martius ex Meisner, Fl. Bras. 5(1): 32, *pl. 12*. 1855.

The holotype in the Munich herbarium bears a tag with the number 838. No collector's number has been cited for this specimen and it is possible that the tag was added at a later date. The specimens at Munich bear several geographic locations on each label and the specific location where these collections were made cannot be determined accurately. The specimen selected as the lectotype is in the best condition and has the most definite locality. It is also the specimen on which the illustration in Flora Brasiliensis is based. However, the fruits of this specimen were all insect-infested

in the field and considerable artistic liberty was taken in depicting them for the illustration. *Coccoloba pipericarpa* is a small-leaved species not clearly defined at present for want of adequate material.

Brazil. BAHIA: Joazeiro, *Martius s.n.* (M–lectotype). MINAS GERAES: Minas Novas, *Martius s.n.* (B, M). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 15357* (B).

Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

In an earlier paper (Jour. Arnold Arb. 40: 89. 1959) I have referred this species to the synonymy of *Coccoloba striata*. The species was based on *Pittier 8880* from Carababo, Guaremales, Venezuela.

Coccoloba plantaginea Weddell, Ann. Sci. Nat. III. 13: 257. 1849.

The type and only collection referred to this species is *Blanchet 1491* (G–holotype, B, NY) from the state of Bahia, Brazil. The specimens I have seen are from lianas, for the stems are tenuous with long internodes. The short lateral shoots bear clusters of leaves and immature inflorescences, all parts of which are densely pubescent. I suspect this species of having a close relationship with *C. crescentiifolia*. Further collections from this area of Brazil will doubtless determine whether both species should continue to be recognized.

Coccoloba populifolia Weddell, Ann. Sci. Nat. III 13: 257. 1850.

In the original description Weddell cited two collections, *Blanchet 1486* and *1646*, from Bahia, Brazil, without designating a type.

Meisner (Fl. Bras. 5(1): 40, *pl. 18.* 1855) referred *Coccoloba alnifolia* Casaretto, an older name, to the synonymy of *C. populifolia* with a question. Lindau saw the Casaretto specimen and accepted the two species as identical (Bot. Jahrb. 13: 198. 1890). I have checked authentic material of both species and agree with this conclusion. I have therefore referred *C. populifolia* Weddell to the synonymy of the older name, *C. alnifolia* Casaretto (*q.v.*).

Coccoloba praecox Herter, Revista Sudam. Bot. 10: 38. 1952.

Herter based this species on his own collection (*Herb. Herter 50852*) made near Arapey, Dept. Salto, Uruguay. The species was characterized by having fascicled flowers which appeared before the leaves. I have seen an isotype in the Paris herbarium. The species can be assigned to the synonymy of *Coccoloba argentinensis* Spegazzini (*q.v.*). *Coccoloba praecox* Herter is a later homonym of *C. praecox* Wright ex Lindau (Bot. Jahrb. 13: 142. 1890).

Coccoloba pubescens L. Syst. ed. 10, 1007. 1759.

Coccoloba grandifolia Jacquin, Enum. Pl. Carib. 19. 1760.

This is a well-defined species of the Caribbean Islands and one which is frequently seen and collected in the large-leaved juvenile form. It is not known from South America, although the older literature contains such references.

Meisner (Fl. Bras. **5**(1): 42. 1855; DC. Prodr. **14**: 152. 1856) in his treatments of the genus gave the distribution as the Antilles, Mexico, British Guiana and Dutch Guiana, and suggested that the species might be expected to occur in Brazil. The report of *Coccoloba pubescens* from Mexico was based on *Schiede 60* which I concluded (Jour. Arnold Arb. **40**: 212. 1959) to represent either an adventitious growth form of *C. liebmannii* or cultivated material of doubtful origin.

The reference to this species in Dutch Guiana is based on *Kegel 1339*. Lindau in his monograph (Bot. Jahrb. **13**: 133. 1890) cited this collection under both *Coccoloba polystachya* var. *pubescens* and *C. pubescens*, although he attributed the latter placement to Meisner. I have not seen the Kegel specimen but Eyma, who did, referred the collection to *C. mollis* (Meded. Bot. Mus. Utrecht **4**: 4. 1932).

The occurrence of *Coccoloba pubescens* in British Guiana is based on Bentham's study of the Schomburgk collection from the upper Rupununi River (Hook. London Jour. Bot. **4**: 624. 1845). I have not been able to locate this specimen, but I question its identification as *C. pubescens* and suggest that it be checked against *C. mollis* or *C. savannarum*.

Coccoloba racemulosa Meisner, Fl. Bras. **5**(1): 30. 1855.

This species was described by Meisner on the basis of an unnumbered Martius collection from Minas Geraes. I have previously referred this species to the synonymy of *Coccoloba declinata* (Vellozo) Martius. *Perrottet 83* from British Guiana which Lindau (Bot. Jahrb. **13**: 168. 1890) cited for this species should be identified as *C. lucidula* Bentham.

Coccoloba ramosissima Weddell, Ann. Sci. Nat. III. **13**: 258. 1850.

Coccoloba laxiflora Lindau, Bot. Jahrb. **13**: 191. 1890.

Lindau described *Coccoloba laxiflora* in his monograph of the genus without any comment on its affinities. The type and only specimen cited is *Glaziou 11444* (B), which consists of one detached mature leaf and several attached leaves which are membranaceous and obviously immature. The type of *C. ramosissima* is *Blanchet 2421*. Lindau separated them in his key on the shape of the leaf base. While all the leaves of *Glaziou 11444* are smaller than those of *Blanchet 2421*, there is little doubt that these species are the same. The type of *Coccoloba laxiflora* was collected in Rio de Janeiro, according to the data on the label, but was

cited from Espírito Santo by Glaziou (Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 571. 1911).

Coccoloba longipes S. Moore (*q.v.*) is similar to the present species. The type collection, *Moore 577*, from the Matto Grosso, represents a rampant shrub or a liana. Both growth conditions are apparent in the specimens I have seen. Moore compared his species with *C. ramosissima* and distinguished it on the basis of larger leaves and longer inflorescences. Additional collections from southern Brazil may clarify the relationship of these species.

Brazil. BAHIA: without location, *Blanchet 2421* (P–holotype of *C. ramosissima*, B, G). RIO DE JANEIRO: without location, *Glaziou 11444* (B–holotype of *C. laxiflora*, C, K).

Coccoloba recurva Newman ex Lindau, Bot. Jahrb. 13: 180. 1890.

Lindau indicated that this epithet was a manuscript name on a specimen in the herbarium at Geneva and published the name in the synonymy of *Coccoloba nitida*. The specimen came from Brazil but the exact locality is not known. A specimen in the general herbarium at Geneva, *Newman 158*, may be the one to which Lindau referred. This is clearly the same as *Coccoloba marginata* Bentham.

Coccoloba riedelii Lindau, Bot. Jahrb. 13: 137. 1890.

Lindau cited only *Riedel 613* in the Leningrad herbarium in his original description, so this specimen must be considered the holotype. A full sheet is now in the Berlin herbarium. The type collection was made at Ilheos, Bahia, Brazil. Lindau distinguished this species from *Coccoloba rosea* Meisner, another species represented by a single collection from the same location as *C. riedelii*, on the size and shape of the leaves. The type specimen of *C. riedelii* appears to represent the mature leaf form and that of *C. rosea* a younger leafy branch; therefore I refer *Coccoloba riedelii* to the synonymy of *C. rosea* Meisner.

Coccoloba rigida Meisner, Fl. Bras. 5(1): 29. 1855.

Coccoloba parvifolia Schott, in Sprengel, Syst. Veg. 4(2): 405. 1827; Lindau, Bot. Jahrb. 13: 175. 1890, not *C. parvifolia* Poiret in Lam. Encycl. 6: 64. 1804.

When *Coccoloba rigida* was described by Meisner, he cited only "*Schott 5538 (912)*" from "Sebastianopolitana" in the Vienna herbarium. The materials of *Coccoloba* in the Vienna herbarium were destroyed during World War II, but a packet containing several leaves and a short piece of the inflorescence from the Meisner herbarium is now at the New York Botanical Garden. The packet bears the annotation "Brasilia (loco non indicato) Schott n 5538 (912) in Hb. Mus. Vindobon." This is the only material of this collection known to me and should be considered the lecto-

type. The fragments are comparable to material of *St. Hilaire 138*, which is more widely distributed.

The name *Coccoloba parvifolia* Schott in Sprengel which Lindau accepted for this species, citing *C. rigida* in synonymy, is a later homonym of *C. parvifolia* Poiret. Poiret's species is correctly identified as *C. microstachya* Willd. I am not certain what is the type of *C. parvifolia* Schott, since no specimens were cited in the original description. Lindau later mentioned four specimens in his treatment of the species but did not designate a type. After the publication of his monograph the Berlin herbarium acquired the Kurt Sprengel herbarium. A scanty specimen from that herbarium bears the annotation "C. parvifolia Schott." Lindau did not annotate this specimen and possibly never saw it. I believe this to be the holotype of *C. parvifolia* Schott. The fragmentary material is comparable to the equally fragmentary holotype of *C. rigida* and it is possible that both species are based on the same collection.

Coccoloba rigida is similar to *C. brasiliensis* but is distinguished from it, at least on the basis of present collections, by its smaller leaves which are obtuse at the base and borne on thin petioles. A dense inflorescence is distinctive in *C. rigida* and the rachis is densely and persistently puberulent.

Brazil. RIO DE JANEIRO: Cabo Frio, *Riedel 683* (TO), *Glaziou 19766* (P), *Schenck 3939* (B); without specific location, *St. Hilaire 138* (B, P). State not known: *Schott 5538* (NY–lectotype of *C. rigida*), *s.n.* (B–holotype of *C. parvifolia* Schott).

Coccoloba rigida Willd. ex Lindau, Bot. Jahrb. 13: 188. 1890.

The epithet "*Coccoloba rigida* Willd." has appeared in several lists of species from South America. Fortunately it has no validity. Lindau cited this epithet as a manuscript name in the synonymy of *C. humboldtii*, a species from Mexico. He indicated that it was based on a specimen numbered 7705 in the Willdenow herbarium. I have not seen this name validly published and certainly hope it never was.

The collection in the Willdenow herbarium numbered 7705 is *Humboldt 4484*, which I have designated as the lectotype of *C. humboldtii* (Howard, Jour. Arnold Arb. 40: 198. 1959). Another specimen of the same number in the Paris herbarium, clearly the same species, bears a label indicating the origin as Vera Cruz and was annotated by Lindau as "*Coccoloba nutans*."

Coccoloba rosea Meisner, Fl. Bras. 5(1): 33. *pl. 14, fig. 2*. 1855.

Coccoloba riedelii Lindau, Bot. Jahr. 13: 137. 1890.

The holotype of *Coccoloba rosea* was collected by Luschnath at Ilheos, Bahia, Brazil, on October 27, 1839. It is the only specimen cited by Meisner and is currently preserved in the Brussels herbarium. The specimen consists of one shoot, obviously a young branch with immature

leaves. Considerable artistic liberty was taken in preparing the illustration published, but there is no question of its being of the Brussels specimen.

The specimens of *Riedel 613* on which Lindau based *Coccoloba riedelii* are more mature and vigorous shoots. They are comparable to *C. rosea* in all details of the inflorescence, pubescence and leaf venation. Only the leaves of *C. riedelii* are larger than those of *C. rosea*. Lindau listed these species successively in his monograph and indicated that *C. rosea* is smaller and more graceful than his new *C. riedelii*. In his key he distinguished them on the conspicuousness of the secondary venation. It is clear to me that the age of the specimens represents the only difference between them and that *C. riedelii* must be considered a synonym of *C. rosea*.

A sterile specimen in the Berlin herbarium, *Sellow 3120* from Brazil, was annotated by Lindau as "*Coccoloba* aff. *pubescens* vel *latifolia*." The specimen has extremely long, hollow internodes. The ocreae are 4–5 cm. long and the petioles arise 1.5–2 cm. above the base. The petioles are 4 cm. long and bear oblong blades 25 cm. long and 18 cm. wide. This specimen appears to me to be an adventitious shoot which should be referred to *C. rosea*.

Brazil. BAHIA: Ilheos, *Luschnath s.n.* (BR–holotype of *C. rosea*, B), *Riedel 613* (LE–holotype of *C. riedelii*, B, BM).

Coccoloba rubiginosa Martius ex Meisner, Fl. Bras. 5(1): 33. 1855.

This epithet was published in the synonymy of *Coccoloba acrostichoides* Cham. by Meisner. The associated collection must be the collection by A. Niermann made in 1832 in Minas Geraes, Brazil. A specimen from the Martius herbarium bearing this name is now in the Brussels herbarium.

Coccoloba rubra L. B. Smith, Jour. Wash. Acad. **45**: 197, *figs. 1–4*. 1955.

Smith attempted to use Lindau's faulty key in comparing his new species with *Coccoloba schwackeana*. A more correct comparison would be with *C. warmingii*. I have seen the types of both species and conclude that *C. rubra* is to be referred to the synonymy of *C. warmingii*. The type of *C. rubra* is the collection made by R. Klein in Santa Catarina, Brazil, bearing the number *Institute of Malariology 33*.

Coccoloba ruiziana Lindau, Bot. Jahrb. **13**: 215. 1890.

Lindau did not indicate a type when he described this species. He cited three collections, *Ruiz & Pavon 228*, which he stated was from Peru, and *Spruce 6340* and *Andersson s.n.*, from Ecuador. The Ruiz & Pavon specimen in the Barbey-Boissier herbarium at Geneva should be designated as the lectotype. It is clearly from the Guayaquil area of Ecuador and not Peru.

Lindau placed this species in his section *Campderia*. However, *Coccoloba ruiziana* is not well defined and field studies are deemed necessary to determine the range of variation to be expected. The specimens cited below are suggestive of *C. obtusifolia* and *C. cujabensis*. From the former, *C. ruiziana* differs in the complete lack of pubescence on the lower leaf surface and in the broader leaf shape. The latter species is defined by the cordate leaf bases and the heavy primary venation. Additional collections are needed to clarify the relationship of these species.

A very pubescent specimen, *Eggers 15526*, is represented by two specimens in the herbaria of the Chicago Natural History Museum and the Berlin Botanical Garden. The specimen from Berlin bears Gross' annotation label with an unpublished specific name referring to "false stipules." The ocreae of the young shoots are often recurved and appear as stipules in this collection and in material of *Coccoloba ruiziana* and *C. spinescens*. The material on hand is inadequate for a reliable description and for the present is considered a pubescent phase of *C. ruiziana*. As such, it becomes intermediate between *C. meissneriana*, *C. obtusifolia* and *C. ruiziana*. It was collected either at Agua Amarga or El Recreo in Ecuador. The two labels carry different data as to location and date of collection.

Ecuador. GUAYAS: Guayaquil, *Ruiz & Pavon 228* (G–lectotype); between Guayaquil & Salinas, *Hitchcock 19989* (GH, NY); Isla Puná, *Andersson s.n.* (B); Posorja, *Mille 786* (F). MANABI: Caracas Bay, *Lehmann BT 748* (NY); El Recreo at Río Mudincho, *Eggers 14929* (F, M, P, US). Locality uncertain: Chanduy, *Spruce 6340* (F, LE, NY, P), Balao, *Eggers 14567* (A, B, LE, M). **Peru.** LAMBAYEQUE: Supo, *Townsend A–135* (F). PIURA: Chulucanas, *Weberbauer 6435* (F, GH); Negritos, *Haught F15* (F). TUMBES: Haciendas Casitas & Ricaplaya, *Weberbauer 7738* (F). Locality uncertain: Talara, *Haught 87* (NY).

Coccoloba sagittata Larranaga, Pub. Inst. Hist. Geog. Uruguay, Escritos 2: 147. 1923.

There is some doubt in my mind whether this was intended to be a new species. Larranaga stated only, "Yo he encontrado la siguiente: 1.a *Coccoloba sagittata* — foliis oblongis sagittatis, angulis posticis brevibus, racimis erectis, compositis. Sp. n. Marzo 19 de 1814." He followed this brief description with a discussion of the properties and uses of the plant which he referred to as climbing and common, and ended with a sentence on the culture of the species. No specimens were cited and none comparable to this description have been seen from Uruguay. The date "1814" may be a typographical error for "1914." The species cannot be identified from the description given and the name cannot be used since there is an earlier homonym by Poiret.

Coccoloba sagittata Poiret, in Lam. Encycl. 6: 64. 1804.

In considering the species excluded from *Coccoloba* for his treatment in Flora Brasiliensis, Meisner cited "COCCOLOBA SAGITATA *Poir.*" and

"Coccoloba sagittifolia *Orl.*" (Fl. Bras. **5**(1): 44. 1855). Both were referred to *Muhlenbeckia sagittifolia* (Ortega) Meisner. I have not seen authentic material but agree that the Poiret species does not belong in *Coccoloba*.

Coccoloba sagittifolia Ortega, Plant. Horti Reg. Bot. Matrit. 60. 1798.

Ortega described fully a specimen growing in the botanical garden at Madrid. Although the native country was given as Brazil, the seed was obtained by Broussonet in Africa. Meisner (Pl. Vasc. Gen. **2**: 227. 1843) first tentatively suggested that the species belonged in his new genus *Muhlenbeckia* and later reaffirmed the placement (DC. Prodr. **14**: 148. 1846).

Coccoloba sagotii Lindau, Bot. Jahrb. **13**: 184. 1890.

The material which Lindau described as *Coccoloba sagotii* is the mature leaf form of *C. lucidula* Bentham. A *Sagot s.n.* collection was cited in the original description and although two specimens of it, both of which are fragmentary, were seen by Lindau in herbaria at Berlin and Stockholm, there is an ample sheet in the Paris herbarium which is an isotype.

Coccoloba salicifolia Weddell, Ann. Sci. Nat. III. **13**: 259. 1850.

This species, which grows as a woody vine, appears to be distinct on the basis of its narrow, lanceolate leaves, although the full range of leaf variation is not known. The type (*Claussen 4*) is in flower. Lindau cited additional Claussen specimens which I have seen and *Schwacke 5801* which I have not seen. Lindau also added a description and illustration of a fruit which may be that of the Schwacke collection. Two additional sterile collections, *Glaziou 3086* and *3090*, have been identified by Lindau as this species. The first collection has larger leaves, considerably different in shape and appearance from the Claussen type. Additional collections and field study of the species is needed.

Brazil. Rio de Janeiro: Nuovo Friburgo, *Claussen 4* (p–holotype, b, br, f, ny), *2002* (ny), *2094* (g); Rio de Janeiro, *Glaziou 3086* (br), *3090* (br).

Coccoloba sarmentosa S. Moore, Trans. Linn. Soc. II. **4**: 446. 1895.

The type collection of this species is *Moore 1038* from Paraguay. It is regarded as a very pubescent phase of *Coccoloba spinescens* Morong and is referred to synonymy there.

Coccoloba savannarum Standley in A. C. Smith, Lloydia **2**: 177. 1939.

This species is still known only from the type *Smith 2225* collected in a scrub savanna in the basin of the Rupununi River in British Guiana. The species appears to be similar to *Coccoloba rosea*, differing in the smaller

ocreae and in having a lax inflorescence with the flowers borne on short pedicels. Both species are inadequately known at present. The type is at the Chicago Natural History Museum with isotypes at the Arnold Arboretum and the New York Botanical Garden.

It is possible that the material collected by Schomburgk from the Upper Rupununi which Bentham referred to *Coccoloba pubescens* (Hook. London Jour. Bot. 4: 264. 1845), may represent adventitious leaves of this species.

Coccoloba scandens Casaretto, Nov. Stirp. Bras. 8: 70. 1844.

Lindau (Bot. Jahrb. 13: 184. 1890) cited this species in the synonymy of *Coccoloba sticticaulis*. Apparently, however, he did not see the type (*Casaretto 76*), for this specimen is cited neither under *C. sticticaulis* nor in his list of specimens studied. The Casaretto herbarium is extant at Turino, but I have not been able to see this specimen. Since Lindau was in error in several other instances where he cited Casaretto species, reducing them without seeing the specimens involved, it seems advisable to list this species without placement at the present time. This reference appears to be the earliest valid publication of the name *Coccoloba scandens*. The specific epithet has been used at least four times in the genus, mostly as *nomina nuda*, for four different species.

Coccoloba scandens Poeppig ex Lindau, Bot. Jahrb. 13: 181. 1890.

Lindau published this epithet (a manuscript name found in the Vienna herbarium) in the synonymy of *Coccoloba peltata* Schott. He did not discuss the disposition of the name, but merely cited the collection *Poeppig 2670* from Ega, Amazonas Province, Brazil. The collections of *Coccoloba* in the Vienna herbarium having been destroyed, it seems worthwhile to call attention to another specimen of *Poeppig 2670* in the Leningrad herbarium. This consists of three detached leaves and a short piece of stem with two very short inflorescence axes, both without flowers. It can be referred to *Coccoloba parimensis* Benth.

Coccoloba schomburgkii Meisner, Linnaea 21: 265. 1848.

Meisner mentioned only *Schomburgk 640* in the original description, but indicated that several specimens were in the Shuttleworth herbarium. Specimens and fragments of this collection are now widely distributed, and a study of a great many of them suggests a variation within the species in the size of leaves and the length of the inflorescences. Numerous recent collections by Steyermark and by Maguire and his associates are available for study and these indicate that, for the present, a very great variation in the habit of the plant and an apparently associated variation in the size and shape of the leaves must be recognized. It is hoped that some future collector in the table-mountain area will be able to determine the range of variation on one plant.

Coccoloba schomburgkii is variously described on collectors' labels as

"shrub 1 foot tall," "small recumbent shrub," "shrub with simple or spreading stems, 3–5 feet tall," "depressed shrub 4 dm. tall," "tree 5–8 m.," "sprawling ligneous vine" or "liana." All of the specimens cited below were collected between 1100 and 2400 meters above sea level. The smaller specimens are reported from "rocky elevations in savannah," while those described as "trees" or "lianas" are reported from the forested edges of savannas, along rivers or on forested slopes. There is a suggestion of a correlation between habitat and leaf size, the plants of the savanna areas or rocky outcrops having the smaller leaves and those of the forested areas having larger leaves. Meisner stated in the original description that the leaves are 1.5–2.5 inches long and 0.75–2 inches wide and heteromorphic on the same branch. Lindau increased the dimensions to 6–10 cm. long and 3–5 cm. broad. The specimens cited below have, within single collections, leaves of the following dimensions: 1.5 × .8 to 4.5 × 2 cm.; 3.5 × 2 to 7.5 × 4.5; 4 × 2.7 to 7 × 5; 8 × 5 to 13 × 8 cm. long and broad. The small leaf-measurements are from the small plants with compact branches and short internodes. The largest leaf-sizes were taken from arching shoots with long internodes, described as a liana. All leaves are coriaceous and in most cases the margin is slightly inrolled. The primary veins depart at right angles, bifurcating near the margin, or are arcuate at slight angles from the midrib. Only one collection has fruit and these are immature. *C. schomburgkii* must be recognized as an extremely variable species as far as leaf size and shape is concerned. The length of the inflorescence appears to vary in proportion to the size of the leaf.

Brazil. AMAZONAS: Territory Rio Branco, Serra Sabang, *B. & C. Maguire 40302* (A, NY), *40433* (A, NY). **British Guiana.** Roraima, *Schomburgk 640 (981)* (K–holotype, B, F, G); Upper Mazaruni river, Imbaimadai Savanna, *Maguire & Fanshawe 32188* (A, NY); between Chinowieng & Chi-Chi landing, *B. & C. Maguire 40663* (A, NY). **Venezuela.** BOLIVAR: Ilu-tepui, Gran Sabana, Mesa Ridge, *Maguire 33402* (A, NY), *33549* (NY); between Enemasic and San Rafael, *Maguire 33596* (A, NY); N.W. of Kavanayen Mission, *Maguire 33741* (A, NY); Ptari-tepui, *Maguire & Wurdack 33900* (A, NY), *33918* (A, NY), *Steyermark 59678* (F), *59712* (F), *60339* (F), *60618* (F); Mount Roraima, *Steyermark 58640* (F), *58676* (F).

Coccoloba schwackeana Lindau, Bot. Jahrb. **13**: 200. 1890.

Coccoloba erecta Glaziou, Bull. Soc. Bot. Fr. IV. **11** (Mem. 3f): 572. 1911, nomen nudum.

This species is readily recognized by the obovate leaves borne on petioles which are inserted well above the base of the ocreae. I have seen no collections, other than the original, which are in fruit. Lindau cited only *Glaziou 14219*, with specimens in the Berlin and Delessert herbaria. This collection has proved to be a mixture with *Glaziou 14220* which is *Coccoloba peltata*. *Glaziou 14219* in the Berlin herbarium is designated as the lectotype.

Brazil. RIO DE JANEIRO: without specific location, *Glaziou 14219* (B–lectotype, C, G, K), *14220* in part (LE, P).

Coccoloba senaei Lindau ex Glaziou, Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 571. 1911.

This epithet was used by Glaziou in a list of determinations of his collections. The name was not published by Lindau, so far as I can determine. Glaziou's description is brief and of no value in the genus. The name should be considered a *nomen nudum* and the species should be referred to the synonymy of *Coccoloba brasiliensis* Nees & Martius (*q.v.*). *Glaziou 19762* and *19763* from Rio dos Pedras, Valu, Minas Geraes, Brazil, were cited by the collector and a specimen of *Glaziou 19763* in the herbarium at Copenhagen has been labeled the cotype. In the Berlin herbarium *Glaziou 19763* and *Schwacke 8005* are both labeled "*Coccoloba senaei* Lindau, n. sp."

Coccoloba sparsifolia Lindau, Bot. Jahrb. 13: 195. 1890.

Lindau based this species on *Don 144* from the state of Maranhão in Brazil. Only a single specimen is indicated and that is in the herbarium at Brussels, although Lindau acquired a fragment which is currently in the Berlin herbarium. I have seen the holotype, which consists of a stem with several short inflorescences and two detached leaves. These leaves are of thin texture, called membranaceous by Lindau, with slender, short petioles. In all aspects the type suggests young specimens of *Coccoloba ascendens*. Lindau separated *C. sparsifolia* and *C. ascendens* in his key to the species on the basis of the glabrous inflorescence axis in the former and the puberulent axis in the latter. However, the type specimen of *C. sparsifolia* does not support this distinction, for the inflorescence axes are as puberulent as those of *C. ascendens*. While additional material may prove it necessary to assign *C. sparsifolia* to the synonymy of *C. ascendens*, I prefer to maintain them as separate species for the present.

Gleason 349 (GH, NY) from the bank of the Potaro River, Tumatumari, British Guiana, is also referred to *C. sparsifolia*. This has ovate leaves, coriaceous in texture, with short, stout petioles. The secondary venation is impressed in the dried condition and the leaf base is conspicuously cordate. Such a combination of characteristics is not familiar to me from the many collections of *C. ascendens* I have seen and from the plants I have studied in the Antilles.

Coccoloba spec. an nova? Herzog, Rijks Herb. Meded. 46: 3. 1922.

The collection *Herzog 1480* made along the Río Piray near Santa Cruz de la Sierra, Bolivia, is completely sterile. Herzog suggested that it might be a new species. The broadly lanceolate leaves are acute at the apex and narrowed to an obtuse base. The petiole is only 2–4 mm. long.

Tufts of brown hairs occur in the axils of the primary veins along the midrib. The specimens are best assigned to *Coccoloba peruviana* (*q.v.*), even though that species is poorly defined at the present.

Coccoloba sphaerococca Lindau, Bot. Jahrb. **13**: 185. 1890.

This species was considered to be similar to *Coccoloba densifrons* Mart. ex Meisner. Both Lindau in his monograph and Macbride (Flora of Peru, Publ. Field Mus. Bot. **13**: 458. 1937) distinguished the two on the basis of venation. The upper leaf surface of *C. sphaerococca* is essentially smooth with the minute venation finely reticulate. The primary veins are not evident. In contrast, the primary venation of *C. densifrons* is evident and when dry the ridged veins are conspicuous by being slightly depressed in the leaf surface.

None of the previous workers has compared this species with *Coccoloba padiformis* Meisner, but while Meisner's species is based on a staminate plant and *C. sphaerococca* is based on a fruiting specimen, it appears to me that only one species is represented. I therefore refer *C. sphaerococca* to the synonymy of *C. padiformis* Meisner. The type is an unnumbered Spruce collection in the Kew Herbarium collected near Tarapoto, Peru.

Coccoloba spinescens Morong, Enum. Pl. 212. 1892; Ann. N.Y. Acad. **7**: 212. 1893.

Coccoloba sarmentosa S. Moore, Trans. Linn. Soc. II. **4**: 446. 1895.
Coccoloba paraguariensis f. *intermedia* Hassler, Repert. Sp. Nov. **14**: 163. 1915.
Coccoloba paraguariensis var. *grandifolia* Hassler, *ibid.*
Coccoloba paraguariensis var. *spinescens* Hassler, *ibid.*
Coccoloba paraguariensis f. *ovatifolia* Herzog, Rijks Herb. Meded. **46**: 3. 1922.
Coccoloba chacoensis Standley, Publ. Field Mus. Bot. **17**: 239. 1937.

This species is typified by *Morong 882* of which I have seen several specimens. In the original description Morong noted that the plant was thorny, the thorns consisting of the sharp, indurated ends of the short branches and branchlets. The leaves are described as oval and elliptic and it is important to note that the petioles were described as "downy." An examination of the type material shows also a characteristic rigidity to the leaves which, when dry, have lighter-colored veins and leaf margins. The pedicels recurve strikingly in fruit and the perianth segments enclose the achene.

Hassler incorrectly associated the species with *Coccoloba paraguariensis*, reducing Morong's species to varietal status. As I have pointed out in the discussion of *C. paraguariensis*, that species must be typified by *Balansa 2060* in the herbarium at Göttingen. The Balansa collection is a mixture and only the Göttingen specimen agrees fully with the original description. The material of *Balansa 2060* in the other herbaria as cited below corres-

ponds with *Morong 882* and therefore must be called *C. spinescens*. There are definitely two species involved.

Hassler described several varieties and forms of "Coccoloba paraguariensis." The typical *C. spinescens* has the smallest leaves. Hassler's forma *grandifolia* (*Fiebrig 4237*) has the largest. Both leaf sizes can be found in single collections and most variations on single specimens. The varieties and forms are of doubtful value unless further field study proves their validity. Gross has annotated other sheets with unpublished varietal names in the Berlin herbarium and such specimens are included in the citations below.

I have assigned *Coccoloba sarmentosa* Moore to the synonymy of *C. spinescens*. The type of Moore's species (*Moore 1038*) is densely pubescent on the lower leaf surface and the inflorescence. The "downy" petioles mentioned by Morong for *C. spinescens* are typical of the species. However, the pubescence extends along the midrib and onto the lamina, as well. Specimens with the amount and density of pubescence on both leaves and rachises to make them intermediate between the types of *C. sarmentosa* and *C. spinescens* are cited below and indicate that *C. sarmentosa* cannot be maintained as a distinctive species.

Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 253. 1959) maintain *Coccoloba chacoensis* Standley as a distinct species, separating it from *C. spinescens* in their key by the absence of lateral branches terminating in spines and by the presence of glands on the lower leaf surface. A tendency to produce terminal spines by modification of the shoot apex is seen on many specimens cited below. The presence of "glands" in *Coccoloba* appears to be inconsistent and unreliable. The "glands," in all cases examined, are either blocked stomata or residual hair bases. Glands comparable to those found on the type of *C. chacoensis* are also on material formerly called *C. paraguariensis* f. *ovatifolia* (*Herzog 1070*), *C. paraguariensis* (*Balansa 2060* in part), *C. paraguariensis* f. *intermedia* (*Hassler 12327*) and *C. paraguariensis* var. *spinescens* (*Rojas 180*).

Bolivia. Chaco, Cururenda, *Cardenas 2529* (FM–holotype of *C. chacoensis*, G); Gran Chaco, Río Pilcomayo, Camoteras, *Herzog 1070* (B–type of *C. paraguariensis* f. *ovatifolia*). **Paraguay.** Asuncion, *Morong 197a* (NY); Chaco, Bahia Negra, *Rojas 13757* (W); Corumba, *Moore 1038* (type collection of *C. sarmentosa*, B, NY); Gran Chaco, Loma Clavel, *Hassler 2486* (A, B, NY); Gran Chaco, *Moore 1049* (NY); Laguna Ypacaray, *Fiebrig 968* (A, M); Puerto Casado, *Pedersen 4027* (A, C); between Río Apa & Río Aquidabán-mi, *Fiebrig 4237* (type collection of *C. paraguariensis* var. *grandifolia*, A, B, GH, M); Río Paraguay, *Balansa 2060* in part (B, P); Río Pilcomayo, *Morong 882* (NY–lectotype, US), *Rojas 180* (B); Ypacaray, *Hassler 11476* (A, GH, NY), *12327* (type collection of *C. paraguariensis* f. *intermedia*, A, GH, NY).

Coccoloba spruceana Lindau, Bot. Jahrb. 13: 162. 1890.

This species was distinguished by Lindau on the basis of its subcoriaceous, subobovate leaves and long ocreae. Since the type collection has only submature leaves, additional collections are necessary to define this species

accurately. No recent collections have been identified with the type collected by Spruce along the Casiquiari in Venezuela. However, the collections cited below are referred to this species. The collection *Maguire, Wurdack and Bunting 36756* was obtained from the classic area of Spruce and was described by the collectors as a tree 8 m. tall. The inflorescences are in bud, yet the leaves appear to be more mature than those of *Spruce 3185*. Considerable variation in leaf size and shape is to be seen on a single branch and the largest leaf can be described as broadly elliptic-oblong with a blade 16 cm. long, 13 cm. broad, rounded at the base and rounded but short-apiculate at the apex. The collections by Ducke, Silverio Level and by Wurdack and Adderley represent still another aspect of the same species. These are all from trees and consist of relatively stout branches of slow growth habit. The leaves, showing considerable variation in size and shape, are well expanded but membranaceous in texture and associated with staminate inflorescences in full flower. It appears that the type collection of Spruce with its obovate leaves represents only one phase of the final concept of this species. The relationship of *Coccoloba spruceana* to *C. striata*, for example, must be re-examined when pistillate flowers and fruiting material are available.

Venezuela. AMAZONAS: rivers Casiquiari, Vasiva and Pacimoni, *Spruce 3185* (GH–lectotype, BR, LE, NY, P); uppermost Río Yatua, *Maguire, Wurdack and Bunting 36756* (A, NY), between Tama-Tama and San Antonio, *Wurdack and Adderley 43652* (A), Cano Yagual on Río Orinoco, *Silverio Level 112* (A). **Brazil.** AMAZONAS: Manaos, *Ducke 21367* (F, NY, Y).

Coccoloba squamosa Martius ex Colla, Herb. Pedemontanum **5**: 48. 1836.

The original description is brief: "7. *C. squamosa*=Mart: in sched: (*Brasil:*) '*C.* caule laeviusculo, foliis brevi-petiolatis ellipticis (longit: 1. latit: ½ pollic:), basi inaequilateris membranaceis integerrimis glabris subtus pallidioribus, racemis axillaribus spicatis nutantibus.' NOB:" Neither Meisner nor Lindau considered this name in their treatments of the genus and I have been unable to locate any specimens, by Martius or others, which bear such a name. The only Brazilian species with leaves of comparable size is *Coccoloba pipericarpa* Mart. ex Meisner, but none of the five Martius collections I have seen of this species bears such a manuscript name. For the present *C. squamosa* cannot be identified.

Coccoloba sticticaulis Weddell, Ann. Sci. Nat. III. **13**: 260. 1849.

Coccoloba longependula Martius ex Meisn. Fl. Bras. **5**(1): 27. *pl. 9*, 1855.

A comparison of the authentic specimens of these species indicates that they are identical and that *Coccoloba longependula* should be referred to the synonymy of *C. sticticaulis*. When Meisner described *C. longependula* he referred to Weddell's *C. sticticaulis*, but indicated that he had not seen material of the type, *Claussen 280*. Lindau also stressed the occurrence of

2 styles in "*C. longipendula*" (sic) in contrast to three styles in *C. sticticaulis*. Unfortunately, such characters are of no value in this genus. Lindau (Engl. Bot. Jahrb. 13: *pl. 5, figs. 34, 37.* 1890) illustrated fruits of both species, describing *C. sticticaulis* as having an ovoid, shortly stipitate fruit, in contrast to the fruit of *C. longependula*, which he described as globose. I have examined all of the specimens cited by Lindau, but not from all the herbaria he listed. There are no fruits available for the specimens I have seen; hence I question Lindau's description of the fruit of *C. sticticaulis*. A study of additional and more recently collected material supports the conclusion that only one species is involved.

A name honoring Claussen is also applied to the Claussen collections I have seen, many of which are without numbers. This name attributed to Weddell, apparently was never published.

Lindau (Bot. Jahrb. 13: 184. 1890) placed the name *Coccoloba scandens* Casaretto (*q.v.*) in the synonymy of *C. sticticaulis* and referred to Meisner's treatments in the *Flora Brasiliensis* and DeCandolle's *Prodromus*. Neither Lindau nor Meisner saw or cited Casaretto's collection. Both authors cited a Riedel collection from Parahyba which I have not seen. Lindau cited *Riedel 2681* and Meisner, *Riedel s.n.* If Lindau is correct in considering *C. scandens* Casaretto identical to *C. sticticaulis* Weddell, then the Casaretto epithet must be used for this species.

Brazil. MINAS GERAES: Bello Horizonte, *L. O. Williams & Assis 6046* (GH); Bento Pires, Bello Horizonte, *L. O. Williams 5285* (GH); Capoeiras, Ouro Preto, *Damazio 1539* (G); Faria, *Glaziou 18427* (A, LE); Lagoa Grande, Municipio Nova Lima, *L. O. Williams & Assis 6577* (GH); Lagoa Pampulha, Municipio Bello Horizonte, *L. O. Williams & Assis 6096* (GH); between Porte do Paraopeba & Chapada, *Martius 759* (M–type of *C. longependula*); without specific locality, *Claussen 280* (P–lectotype of *C. sticticaulis*, (G), *s.n.* (A, GH); *Glaziou 21979* (BR). RIO DE JANEIRO: Caxoeira do Campo, *Lund 35* (B); Caxoeira do Campo, Lazoa Sta., *Warming 130* (C, LE); Restinga do Jacarépaguá, *Brade 77* (GH); Serra do Piedada, *Warming 126* (NY); Sta. Luzia do Rio das Velhas, *Schwacke 11431* (B).

Coccoloba striata Bentham in Hooker, London Jour. Bot. 4: 626. 1845.

Coccoloba grisebachiana Lindau, Bot. Jahrb. 13: 195. 1890.
Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

Bentham based this species on a collection by Schomburgk from British Guiana. Although a specific locality is not given, Lindau thought it to be near Roraima and one herbarium label refers to the "savannah." The collection was made in April, 1843, and bears the second collection numbers 929 or 1265.

Coccoloba grisebachiana Lindau, based on *Crueger s.n.* from Trinidad, and *C. pittieri*, based on *Pittier 8880* from Venezuela, were placed in the synonymy of *C. striata* in an earlier paper (Jour. Arnold Arb. 40: 89. 1959).

The relationships of *Coccoloba glaziovii*, *C. parimensis*, and *C. spruceana*

with the present species are not clear. Additional material and field study may show these to be representatives of only one species.

British Guiana. Roraima area, *Schomburgk 929* (P), *1265* (B, P). **Venezuela.** ANZÓATEQUI: El Amparo de Chive, *Pittier 15025* (US); Guaremalos, Punta Cabello San Felipe, *Pittier 8880* (type collection of *C. pittieri*, A, GH, LE, NY). FEDERAL DISTRICT: Carruao, *Pittier 11847* (A, GH, NY).

Coccoloba stricta Klotzsch in Schomburgk, Fl. Faun. Br. Guy. 934. 1848; Lindau, Bot. Jahrb. **13**: 167. 1890.

Lindau referred this name, published without description, to the synonymy of *Coccoloba lucidula*. Of the Schomburgk collections I have seen and identified as *C. lucidula*, none has such a manuscript name.

Coccoloba strobilulifera Meisner, Fl. Bras. **5**(1): 25. 1885; Howard, Jour. Arnold Arb. **40**: 185. 1959; Lindau, Bot. Jahrb. **13**: 193. 1890.

Coccoloba strobilulifera was based on *Moritz s.n.* (*type*–P), collected in Colombia but without a known specific locality.

Meisner recognized that *Coccoloba strobilulifera* was similar to *C. acuminata* HBK., but stressed the differences in pubescence, shape of leaf bases and length of inflorescences in establishing and maintaining the species. Lindau placed the species in the synonymy of *C. acuminata*, but described a new variety to accommodate it. The numerous collections I have cited previously (*loc. cit.*) as *C. acuminata* (*q.v.*) show gradations to indicate that *C. strobilulifera* cannot be maintained as a distinct species or variety.

Coccoloba sublobata Heimerl, Denkschr. Akad. Wiss. Wein. **79**: 244. 1908.

This species has been referred to the synonymy of *Coccoloba glaziovii* (*q.v.*) and discussed there. The type was in the collections at Vienna and was lost during World War II. However, a photograph of this specimen is in the collections of the Chicago Natural History Museum and a duplicate specimen bearing the same number but a different unpublished binomial attributed to Heimerl is in the Berlin herbarium. The type collection is *M. Wacket 12*, made in 1902 near Santos, Serra do Cubatão, São Paulo, Brazil.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Howard, Jour. Arnold Arb. **37**: 324. 1956.

The type locality of this species is Jamaica. Continuous but slight variations occur in collections made in the Antilles, from Jamaica southward to St. Lucia and Barbados, and in Central America, specifically in British Honduras and Honduras. The species has not been collected in Grenada, Trinidad, or Tobago or in Central America south of Honduras. The following collections from Curaçao, Aruba, and mainland Venezuela

fit into the known range of morphological variation but represent a disjunction of the range of the species. Future field studies of the populations represented by the specimens cited may indicate a hybrid situation or that a subspecific category is desirable.

Aruba: *Boldingh 6384* (NY). **Bonaire:** *Boldingh 7051, 7489* (NY). **Curacao:** *Boldingh 4882, 5070* (NY); *Britton & Shafer 3082* (NY); *Curran and Haman 150, 234* (NY); *Realino 18* (NY). **Venezuela.** PARAGUANÁ: Cerro Santa Ana, *Curran & Haman 525, 539* (GH), *702* (GH, NY); Pueblo Nuevo, *Tamayo 930* (GH).

Coccoloba tenuiflora Lindau, Bot. Jahrb. 13: 190. 1890.

Lindau described this species and mentioned that he saw a specimen in the Leningrad herbarium. He noted that the specimen was in flower in April, that it had been collected in Brazil, and that neither the specific location nor the name of the collector was indicated. In the material on loan from Leningrad I find a single sheet bearing the name "C. tenuiflora Lindau." The three fragments on this sheet are from the Fischer herbarium and one of the three labels on the sheet suggests that the plant may be cultivated. Nearly all of the material of the genus which I have seen from the Fischer herbarium has been of cultivated plants. Although several words cannot be deciphered, no date is given on any of the labels. There is also a second sheet in the Leningrad herbarium which was not annotated by Lindau but which is clearly the same plant. The label on this sheet states that the specimen is from a cultivated plant. The typification of this species is difficult. Lindau apparently obtained a fragment from the Leningrad sheet which he cited and the fragment plus a drawing is in the Berlin herbarium, though this was not cited in the original description. The sheet in Leningrad which Lindau cited has several fragments, plus additional material in packets; these could have come from one plant or from several or could have been taken at different times. However, it appears necessary to designate the sheet in Leningrad as the holotype.

Coccoloba tenuiflora Lindau is poorly understood. The species appears to be similar to *C. longipes* from the Matto Grosso, but the effects of greenhouse cultivation on *C. tenuiflora* are difficult to evaluate. The plants are obviously deciduous in cultivation, for some specimens show a flush of immature and delicate membranaceous leaves and ocreae on elongated shoots. Lindau concluded that the oblong to obovate leaves with long, acuminate apices and the elongated pedicels distinguish the species.

Coccoloba tiliacea Lindau, Bot. Jahrb. 13: 198. 1890; Buchinger & Sanchez, Bol. Soc. Argent. Bot. 7: 255. 1959.

Coccoloba peltata Griseb. Symb. Fl. Argent. 508. 1879, not Schott.

This species is easily recognized and is well represented in herbaria by material from northeastern Argentina and Bolivia. The plants are small trees with broadly ovate leaves which are commonly crenate or undulate

at the margins. The leaves vary from peltate to non-peltate on the same specimens. The base of the blade may be obtuse and slightly to deeply cordate. The blades may show all gradations from attachment at the margin to peltation, with as much as 2.5 cm. of lamina between the petiole point of attachment and the margin. The inflorescence may be simple or much branched. The inflorescence branches usually arise from the base and may give the appearance of a cluster of racemes of equal length. The fruit has imbricate, but non-coronate perianth lobes one-third the length of the fruit.

In the original description Lindau cited several specimens without indicating a type. *Lorentz & Hieronymus 499* (B) has been designated as the lectotype.

Argentina. JUJUY: Ledesma, Sierra de Calilegua, *Venturi 5355* (A, F, GH); San Pedro, Sierra Santa Bárbara, *Venture 9655* (A, GH, LE, NY); San Antonio near San Lorenzo, *Lorentz & Hieronymus 378* (B, GOET), *Schulz 8169* (B, NY). SALTA: Orán, Badahonda, *Lorentz & Hieronymus 446* (GOET, NY, S), *499* (B–lectotype, GOET), Cuesta de Santa Rosa, *Lorentz & Hieronymus 658* (B, NY), El Bananal, *Meyer 658* (B, NY), Quinta del Río Santa María, *Willink 127* (W), Río Bermejo, *Schreiter 218* (F), Río Colorado, Paso Hondo, *Meyer 6492* (W), Tartagal, *Schreiter 3696* (GH), *8462* (GH), *11471* (A), *Venturi 5176* (A), Vado Hondo, *Devoto & Alberti 2223* (A). TUCUMÁN: Capital, cultivated, *Meyer 15813* (BR, W). **Bolivia.** LA PAZ: Sierra de Aguaragra, *Troll 304* (B). SANTA CRUZ: Between Santa Cruz and Samaipata, *Cardenas 4631* (US). TARIJA: La Merced, near Bermejo, *Fiebrig 2178* (A, M).

Coccoloba trianaei Lindau, Bot. Jahrb. **13**: 213. 1890.

This species is known only from the type collection, *Triana 974*, with the holotype in the Berlin herbarium and one isotype at Brussels. The collection was made in Colombia but no specific location or altitude data are given. The specimens are from staminate plants and the inflorescence tends to produce several shorter branches from near the base.

Coccoloba trianaei is similar to both *C. lehmannii* and *C. venosa*. It differs from *C. lehmannii* in having more lanceolate to ovate-lanceolate leaves with abruptly rounded bases and much shorter petioles. The stems, leaves and inflorescences are slightly more pubescent than in comparable material of *C. lehmannii*. In size and shape, the leaves of *C. trianaei* are similar to many specimens of *C. venosa*; however, the amount of pubescence and the laxly flowered inflorescence differs from that of *C. venosa*. Additional collections of *Coccoloba* are needed from coastal areas of Colombia to determine whether *C. trianaei* is only a pubescent phase of *C. venosa* or a truly distinct species.

Coccoloba uvifera (Linnaeus) Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.

The common "sea grape" or "uva" is a well-known tropical American tree of the seacoast areas. It is abundant in the Caribbean, yet it has been

overlooked there by many collectors so that herbarium records of its distribution show many gaps where it might be expected to occur.

In the present study it is of interest to note that the species is not represented in collections from Brazil or southern South America. Meisner mentioned the species in his treatment for *Flora Brasiliensis* (**5**(1): 42. 1855) without seeing specimens and questioned the identification of specimens to that species cited by other authors.

Colombia. ANTIOQUIA: Medellín, *Daniels s.n.* (NY). ATLÁNTICO: Puerto Colombia, *Barkley & Gutiérrez 1859* (F). BOLÍVAR: Boca Grande near Cartagena, *Killip & Smith 14092* (A, GH, NY); Torrecilla near Turbaco, *Killip & Smith 14418* (A, GH, NY). MAGDALENA: Barranquilla, *Holton s.n.* (NY); Santa Marta, *H. H. Smith 2102* (A, NY). Department not indicated: Gaira, *Castañeda 54* (F). **Curaçao.** *Curran & Haman 53* (A). **Dutch Guiana.** Without location, *Weigelt s.n.* (LE); *Regel 984* (NY). **Venezuela.** FALCÓN: Cumarebo, *Curran & Haman 491* (GH, NY), *492* (GH). FEDERAL DISTRICT: Caracas, *Pittier 10343* (GH, NY); La Guaira, *Fendler 840* (GH, NY); Macuto, *Pittier 11791* (A, NY). SUCRE: Cristóbal Colón, *Broadway 594* (GH, NY). Without location: *Mocquerys 800* (A, NY, P).

Coccoloba uvifera Salzman ex Lindau, Bot. Jahrb. 13: 186. 1890, not Linnaeus.

This epithet is a manuscript name on several Salzman collections, although Lindau referred specifically to the one in the Delessert herbarium. Lindau appears to have been the first to publish the name in the synonymy of *Coccoloba laevis* Casaretto. I have discussed the Salzman collections under *C. laevis*.

Coccoloba vellosiana Casaretto, Nov. Stirp. Bras. 70. 1844; Howard, Jour. Arnold Arb. **41**: 43. 1960.

In an earlier study (*loc. cit.*) I placed this epithet in the synonymy of *Coccoloba arborescens* (*q.v.*). Although Casaretto cited an unnumbered Riedel collection in the original description, he also indicated that his new species was a transfer of *Polygonum frutescens* Vellozo. *Coccoloba vellosiana*, therefore, must also be rejected as an illegitimate name.

Coccoloba venosa Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

The complexities of this name, along with the problems of the morphology and distribution of the species, have been discussed by Fawcett and Rendle (Jour. Bot. **51**: 123. 1913) and by me (Jour. Arnold Arb. **30**: 398. 1949; **40**: 217. 1959). The specimens cited below are typical of the Lesser Antillean expression of the species, with the sole exception of *Velez 2668* which is similar to material from Central America formerly called *Coccoloba floribunda*.

Colombia. META: Puerto López, *E. L. & R. R. Little 8416* (NY). **Venezuela.** APURE: Puerto Páez, *Velez 2668* (US). SUCRE: Cristóbal Colón, *Broadway 431* (GH), *664* (GH, NY). YARACUY: Aroa, *Curran 323* (NY).

Coccoloba virens Lindley, Bot. Reg. 21: *pl. 1816*. 1835; Howard, Jour. Arnold Arb. 41: 41. 1960.

This species was based on greenhouse material of unknown origin presumed to be from the West Indies. As I have pointed out, Lindau placed the species incorrectly. The correct disposition is to regard *Coccoloba virens* as a synonym of *C. coronata* Jacq.

Coccoloba warmingii Meisner in Warming, Symbollae 128. 1870.

Coccoloba rubra L. B. Smith, Jour. Wash. Acad. Sci. 45: 197, *figs. 1–4*. 1955.

This species of southeastern Brazil is recognized by the obovate leaves which are bullate between the veins. The leaf apex is rounded, emarginate or abruptly mucronate in immature leaves but all mature leaves showed abnormal development of the apex.

No specimens are cited by number in the original description where Meisner stated, "Hab. in Serra da Gamba et in prov. Rio de Janeiro, m. Maio legit Warming." Lindau (Bot. Jahrb. 13: 200. 1890) cited only specimens in the Warming herbarium but referred to these by numbers *125* and *128*. There is a fragment of an inflorescence, a single detached leaf and a sketch of an attached leaf of *Warming 125* in the Berlin herbarium. The origin of this fragment is not given. Specimens of both *Warming 125* and *128* are to be found in the Copenhagen herbarium where the first sheet is labelled "co type" and its origin indicated as "Rio." *Warming 128* (collected at Serra da Gamba) in the Copenhagen herbarium should be the lectotype.

Smith suggested that his new species *Coccoloba rubra* would be near to *C. schwackeana* in Lindau's key to the genus. Lindau's key, however, is faulty and it is difficult to reach *C. warmingii* with the material Lindau preserved in the Berlin herbarium. It is clear that *C. rubra* is a synonym of *C. warmingii.*

A single sterile specimen of *Burchell 3982* in the Kew herbarium appears to represent the adventitious leaf form of this species. Although Lindau referred this collection to *Coccoloba latifolia*, the elevated origin of the petiole on the ocrea indicates that the collection is better assigned here. *Dusen 17225* cited below is a similar sterile collection.

Brazil. Minas Geraes: Piedade a Santa Luzia, *Glaziou 20438* (b, le, p); Santa Luzia do Rio das Velhas, *Schwacke 11430* (p). Rio de Janeiro: Rio de Janeiro, *Warming 125* (b, c); Serra da Gamba, *Warming 128* (c–lectotype, b). Santa Catarina: Mato do Hoffmann, Brusque, *Klein s.n.* (Instituto de Malariologia 33) (us–type of *C. rubra*). São Paulo: Jacarehy, *Dusén 17225* (gh).

Coccoloba williamsii Standley, Publ. Field Mus. Bot. 11: 148. 1936.

The type of this species in the Chicago Natural History Museum is *Llewelyn Williams 4803* from Peru. I have referred this species to the synonymy of *Coccoloba lehmannii* Lindau in an earlier paper (Jour. Arnold Arb. 40: 200. 1959).

Coccoloba zernyi Standley, Publ. Field Mus. Bot. 22: 18. 1940.

The type and apparently the only specimen of this species was collected by Ginzberger and Zerny between Taperinha and Santarem in Amazonas, Brazil, Aug. 13, 1927. It consists of two flowering branches and a few detached leaves in a packet. The inflorescence is very pubescent and all the flowers examined were staminate, lacking even the rudiments of a pistil. There is little doubt that this species is more properly assigned to the genus *Ruprechtia*; * however, the material available is inadequate for reference to any known species. It is hoped that some future monographer of *Ruprechtia* may find the correct assignment for this specimen.

* **Ruprechtia zernyi** (Standley) Howard, comb. nov. *Coccoloba zernyi* Standley, Publ. Field Mus. Bot. 22: 18. 1940.

VEGETATION ON GIBBSITIC SOILS IN HAWAII

J. C. Moomaw and M. Takahashi

Studies of the vegetation of an area of highly aluminous soils on the island of Kauai were initiated early in 1958. The soils were being considered by several aluminum companies as a commercial source of bauxite and the studies on rehabilitation of land denuded by strip mining were undertaken at the request of the then Territorial Legislature by the Hawaii Agricultural Experiment Station.[1] The purpose of the studies was to accumulate the ecologic, soil, and agricultural information that would enable the Legislature to enact suitable and just laws governing the reclamation of the mined area following removal of the mineral. It is the purpose of this paper to report studies of the initial vegetation of the reclamation study site made before the simulated mining and reclamation studies were begun. These studies represent the basic floristic and ecologic data with which comparisons of the reclamation treatments and results will be made. Coöperation in parts of the research was provided by several other departments of the Territorial government, especially the Board of Commissioners of Agriculture and Forestry, the Territorial Commissioner of Public Lands, and the B. P. Bishop Museum. Voucher specimens of the plants collected were deposited in the Bishop Museum and retained for study in the University of Hawaii Department of Agronomy and Soil Science.[2]

The site of the major investigations is an area of about 2500 acres located six miles WSW of Kapaa, Kauai, in the Wailua Game Refuge and adjacent lands. (The elevation varies from 500 to about 2000 feet.) Brief reference will be made to areas on Maui and Hawaii that were briefly examined and from which plant collections were made for determinations of tissue aluminum levels (Moomaw *et al.*, 1959).

Major studies of the vegetation of aluminous soils have been made in Australia–New Guinea (Webb, 1954) and in Jamaica (Howard & Proctor, 1957). In the Australia–New Guinea flora, 69 of 1154 dicotyledonous species examined were classified as accumulators of aluminum, as were 11 of 87 pteridophytes and *Lycopodium*. No monocotyledons or gymnosperms were so classified of 69 and 14 species respectively examined. The information developed by Webb in this study was used primarily for taxonomic deductions concerning the flora and the evolutionary status

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station, University of Hawaii, as Technical Paper No. 483.

[2] Appreciation is expressed to Marie C. Neal, Curator of the B. P. Bishop Museum Herbarium, and to E. Y. Hosaka, Hawaii Agr. Extension Service, for help with the identification of some of the specimens.

of its members and secondarily for biochemical and ecologic discussions. Aluminum accumulating plants were never found on alkaline soils but were restricted to leached, acid soils from a variety of parent materials. Most of the species were inhabitants, with exceptions, of the closed mesic forest formation in eastern Australia which is in accord with the work of others (Chenery, 1948, 1949), who have observed the high frequency of aluminum accumulator species in the floras of the moist tropics. Webb states aluminum accumulators to be striking examples of what Crocker (1952) calls "pedogenetically effective biotypes" in that they favor laterization by the accumulation and retention of aluminum in the surface layers of the soil and in the litter and organic matter. Evidence from Webb (1954) and from Chenery (1948, 1949) indicates that accumulation is relatively rare in the monocotyledons but the information from Hawaii's gibbsitic soils given by Moomaw *et al.* (1959) shows substantial levels of the element in the dominant grasses, (especially *Paspalum orbiculare*), several other grasses, and the ground orchid *Spathoglottis plicata*.

The extensive work of Howard and Proctor in Jamaica (1957) led to conclusions that the Jamaican bauxite soils supported few species of aluminum accumulators and that the bauxite flora consisted of plants unaffected by aluminum and tolerant of its presence. They found no species characteristic of bauxite soils and did not find any species on adjacent soils that would not grow in the bauxite deposits. Their examination of a large flora in an area of active mining included successional studies on fallow mining pits and replanting plots with woody and pasture species.

GEOLOGY AND SOILS

The parent rocks of the Wailua Game Refuge are part of the Koloa volcanic series which flowed from vents in the mountain range to the north (MacDonald *et al.*, 1954) and the soils derived from these low-silica melilite and nepheline basalts have been described by Sherman (1958) and Cline *et al.* (1955) as belonging to the Aluminous Ferruginous Latosol and Ferruginous Humic Latosol great soil groups. The principal soil series in the area are the Halii, Puhi and the Haiku. The Halii series, in the Honolua family, is described by Cline *et al.* (1955) as being three to four feet in depth with dark brown, strongly granular, gravelly, silty clay at the surface grading into reddish and yellowish-red, blocky, silty clay at the depth where weathered rocks that have retained most of their original structure are frequently encountered. The soils are strongly acid (pH 3.5 to 5.0) and generally occur on long, smooth, narrow ridges of gentle (3–8%) slope but with steep-sided (40–50% slope) narrow gullies between them.

The chemical weathering of these soils from their porous, fine-grained parent rock is stated to be typical of many of the bauxite areas of the world and has been exceedingly rapid (Sherman, 1958; Mohr & Van Baren, 1954) because: (1) easily soluble minerals are present that are relatively free from combined silica and almost totally free from quartz;

(2) the topographic position, high effective rainfall at the higher elevations, combined with the high infiltration rate, free circulation and lateral movement of the percolating water favor the reduction and leaching of the iron oxides; (3) the humus of the forest floor produces an acid soil solution (Sherman & Kanehiro, 1948) which hastens the leaching process; and (4) a long period of chemical weathering has brought about the decomposition of silicates and the subsequent desilication of the weathering zone. The product of this intense and lengthy weathering process is a group of strongly leached soils depleted of bases and silica (0–5% SiO_2) with high concentrations of iron (25–60% Fe_2O) and alumina (20–50% Al_2O_3) and with at least small amounts of titanium (3–6% TiO_2). The principal mineral in the clay fraction developed under these conditions has been identified as gibbsite (Sherman, 1958).

Much evidence of mineral deficiency, especially of phosphorus, is observed in the vegetation. The surface soils are low in total bases but high in total nitrogen and organic matter. Physically the soils are classed as clays but do not in general display the physical properties usually associated with clays. Even when moist the soils present no physical problem in tillage operations.

THE CLIMATE

The mean annual rainfall has not been accurately measured on the main research site but it is known from adjacent areas to vary between 50 and 150 inches and to be well distributed. In general, the mean rainfall is greater than three inches per month and more than five inches per month during seven to twelve months of the year, with more than ten inches falling during two to seven months. The effectiveness of the rainfall is high and the soils are dry for only a few months in the lower areas. The rainfall exceeds evaporation and transpiration, especially during the winter months, partly because of a high degree of cloudiness. Relative humidity is high. Data for the nearest long-term weather station, Kapaa Stables, are given in Table I.

The average air temperature at sea level is about 73° F. in this zone, which is two or three degrees lower than that in the dry regions and, of course, it decreases with elevation. Extreme temperatures seldom exceed 90° F. or fall below 55° F. A long-term record of temperature for the northeast shore of Kauai is shown in Table I.

Wind blows almost constantly from the northeast at 10 to 20 miles per hour and exerts a drying influence on the exposed ridge-tops but frequently brings the trade showers to these same parts of the landscape. Hurricanes have been known in the area only recently and wind velocities of 75 or 80 miles per hour have been recorded. In the Islands the trade winds diminish and sometimes fail completely during and just after the autumnal equinox.

Daylength at 21° N. Latitude varies about 2.7 hours from June to December.

TABLE I. Mean Monthly Temperature and Rainfall Data for Nearby Stations (Weather Bureau, 1959).

STATION	Kapaa Stables	Kealia
ELEVATION	175 feet	9 feet
YEARS OF RECORD	18	47
	PRECIPITATION	TEMPERATURE
January	6.36 inches	70.9° F.
February	5.91	71.1
March	6.14	71.6
April	4.47	73.2
May	2.64	75.0
June	2.03	77.1
July	2.46	78.1
August	2.82	78.9
September	2.41	78.6
October	4.81	77.4
November	5.95	74.9
December	6.21	72.7
Annual	52.21 inches	75.0° F.

LAND USE AND HISTORY

At present, most of the land in the Honolua soil-family is used for either pasture or forest production. In neither case is the production potential high. The forest is composed mostly of *Meterosideros collina* ssp. *polymorpha* (ohia lehua) which is not of merchantable size. The forage produced is considered to be of inferior quality because of apparent low dry-matter production, low palatability, and probable mineral deficiencies. Shrubby weeds are a constant source of trouble in these areas. There is evidence that applications of lime and fertilizer will greatly improve production and nutritive value of the forage. The pastures are generally used for breeding herds and not for fattening cattle except when improved species such as *Digitaria decumbens* (Pangola grass), *Pennisetum clandestinum* (Kikuyu grass), or *Pennisetum purpureum* (Napier grass) have been planted. Paspalums, especially *P. conjugatum*, are naturalized pasture species of fair value. Very little land area of this type is cultivated at present, the high degree of cloudiness limiting sugarcane production and the wetness restricting its use for pineapple culture. Since the climate is continually moist, the control of diseases, insects, and weeds is extremely difficult. Little of the area is used for vegetable crops or fruit production but current research shows that this can be changed in many cases by improving fertility.

The land-use history of the Game Reserve of Kauai is one of hard use and abuse with a relatively recent attempt at reclamation through reforestration and game-food planting. The primeval vegetation was almost certainly forest but the composition of the forest is difficult to reconstruct

after nearly 200 years of agricultural use by European and American settlers. The 900–1000 years of Hawaiian settlement had relatively little effect on this area since their settlements were normally confined to the beaches and the broad open valleys at low elevation. No remnant of terraces or native artifacts was encountered in the Game Reserve and such important native food plants as breadfruit, cooking banana and *Alocasia macrorrhiza* (ape) were absent.

The three major phases in the history of the Hawaiian flora were: (1) the arrival of the Hawaiians with their food plants and limited cultivation; (2) the introduction of European agriculture, forestry (especially the sandalwood trade) and cattle about 1790; and (3) the continued introduction of useful and weedy plants that have readily naturalized in the Hawaiian Islands. Especially the second and third of these influences have had a major effect on the Hawaiian vegetation in all ecologic zones and have led to replacement of the indigenous vegetation to a major degree by exotic species (Degener, 1932–date; Neal, 1948).

The vegetation of the Game Refuge of Kauai is classed in zone D_2 by Ripperton and Hosaka (1942) and was originally forested. The vegetation is dominated by *Metrosideros collina* subsp. *polymorpha* (ohia lehua) which is associated with *Acacia koa* (Hawaiian koa) and *Psidium guajava* (guava) in most places. Ferns such as *Dicranopteris linearis* (false staghorn), *Sadleria cyatheoides* (amaumau), *Nephrolepis exaltata* (Boston fern), and the tree fern *Cibotium chamissoi* are frequent. *Pandanus sp.* (hala) and *Aleurites moluccana* (kukui) are abundant in some areas and *Stachytarpheta cayennensis* (joee) is a weed of nearly universal occurrence. Open areas are dominated by grasses, sedges, herbs and several of the smaller ferns mentioned above. *Paspalum conjugatum* (Hilograss), *P. orbiculare* (ricegrass), *Setaria geniculata* (yellow foxtail) and a few others are found, and *Axonopus affinis* (carpetgrass) and *Sporobolus capensis* (rattail grass) are becoming more widespread. *Cyperus spp.* (sedges), *Centella asiatica* (Asiatic pennywort), *Mimosa pudica* (sensitive plant), and *Cuphea carthagenensis* (tarweed) are among the usual herbs.

The original forest on the reclamation site was probably a *Metrosideros* overstory with the tree fern *Cibotium chamissoi* either as the ground cover or at least well represented in the understory. The tree cover was probably relatively open on the ridge-tops. Whether the *Acacia koa* or *Santalum freycenetianum* (sandalwood) were ever represented here cannot be determined from present evidence, but is unlikely. The *Acacia* may have extended to this low elevation at one time. *Aleurites moluccana* (kukui) and *Eugenia malaccensis* were dominant in the valley-bottoms and drainages, but during the past hundred years these have been largely replaced by the more aggressive *Psidium guajava*, introduced in 1835. They show evidence of regeneration as does the *Metrosideros* on higher slopes.

The date of the first destruction of the forest cover on the Game Refuge

is difficult to place but it can be said with certainty that since World War I the area has been repeatedly burned and at least lightly grazed. From 1918 to 1938, a major part of the area was leased as public grazing land, prior to which it had been in the Forest Reserve. There is no evidence of pasture improvement practices other than fencing, and it is known that the carrying capacity for livestock was very low. Species of improved pasture grasses and legumes are absent.

In 1939 the Wailua Game Refuge was created and management passed to the Division of Fish and Game of the Board of Agriculture and Forestry. Grazing was immediately prohibited and attempts were made to improve the cover and food supply for introduced species of game birds. During World War II, the Refuge was turned over to the military for a training area and was used for maneuvers, bivouac, and as an artillery range. Coral sand was brought in for camp sites and many of the ridges were travelled by military vehicles. The higher elevations were used as the impact area for an artillery range, which caused repeated fires. The lower, drier parts of the Refuge were much more easily fired than the higher parts but even on the slopes of Mount Waialeale to the west, where the annual rainfall probably exceeds 250 inches, the burned snags of *Metrosideros* trees of 18-inch diameter can be seen.

The area of study is traversed by an irrigation-ditch system involving a series of tunnels and ditches in some of the valleys but no direct influence on the vegetation is involved.

About ten years ago, after the end of the war, the Board of Agriculture and Forestry instituted a trial planting on a part of the area involving macadamia nut, Norfolk Island pine, and the variegated *Pandanus variegatus* (hala). Some of the planted trees have survived and are making slow growth. On a small plot of about an acre, the Board planted *Cajanus cajan* (pigeon pea) after plowing, liming with 500 pounds of crushed coral and fertilizing with 150 pounds of superphosphate per acre. The effect of this treatment is still visible on aerial photographs and can be seen on the ground from a distance of about a mile.

It is also interesting to conjecture on the role of wild goats in the destruction of native forest in this area and its subsequent displacement by introduced species.

VEGETATION OF GIBBSITIC SOILS

Methods

After an initial reconnaissance and examination of aerial photographs, the immediate surroundings of the test area were analyzed by examining a series of seventeen 100-foot line transects. Seven of the transects were oriented parallel with the center-line of the main ridge and on it, two were transverse transects on the ridge top, and eight of the transects were in pairs on the generally north- and south-facing slopes about one-third of the slope distance from the ridge-top and the valley-bottom respectively.

On each transect, *cover* was estimated on 50 two-square-foot plots evenly spaced along the line. Cover was estimated directly for each species present to the nearest five per cent and *frequency* was calculated from the cover data. Cover and frequency are commonly used ecologic measures of the importance of species in the plant community and of their distribution and dominance (Braun-Blanquet, 1932; Brown, 1954).

As used in this study, cover is best defined as the percentage of the total soil area covered by living plant material when it is projected downward into the plane of the soil surface from its natural growing position. It is always taken as the maximum spread of the plant involved, ignoring minor discontinuities in the crown or aerial portions. Since the objective of the method is to give a measure of the relative dominance of the species among its competitors, foliar spread is accepted as a good relative measure of root spread which is also an important factor in competitive domination.

Frequency is simply the percentage of the total number of plots in which the species occurred. This frequency of occurrence is a better measure of distribution within a subsample than is cover since it tends to be independent of plant size and dominance.

The parts of the Reserve not included in the quantitatively measured associations, such as the valley-bottoms and stands of pure *Dicranopteris* on steep slopes, were examined with long walking transects or jeep traverses resulting in species lists on which the only notations were of observational frequency, dominance, age, size, and general habitat and distribution.

Species Distribution

From the transect data in TABLE II and the general reconnaissance of the much wider area, including other ridges, the valley bottoms, and the higher elevations of the study site, it is possible to arrange the vegetation into three distinct and more or less homogeneous plant communities. The first and most general of these is the *Setaria–Paspalum* (weedy grass–shrub) association on the ridge-tops and exposed south slopes. On the northeast slopes extending nearly to the bottoms and occupying the northeast edge of the ridge is a community of weedy grasses and ferns designated as *Setaria–Nephrolepis* association. In the valley-bottom, a riparian, or at least much more mesic association of small trees, ferns and associated species is found. None of these communities approaches a climax type and each of them is a degraded representation of a collection of introduced species, each on a different habitat type.

The *Setaria–Paspalum* association of the ridge-top is a common one in the high-rainfall zone in the Hawaiian Islands and is similar to the vegetation associated with another known bauxite area on Maui (Haiku). As shown in TABLE II, this association is dominated by several common weedy grasses, *Setaria geniculata*, *Paspalum orbiculare*, and herbs such

TABLE II. Mean Cover and Frequency Percentage in Two Associations on Gibbsitic Soils of Kauai.

SPECIES	ASSOCIATIONS			
	SETARIA–PASPALUM (13 transects)		SETARIA–NEPHROLEPIS (4 transects)	
	Cover	Frequency	Cover	Frequency
Grasses				
Setaria geniculata	62%	99%	82%	99%
Paspalum orbiculare	38	82	20	58
Sacciolepis contracta	17	58	30	71
Chrysopogon aciculatus	7	21	2	6
Paspalum conjugatum	6	17	1	3
Ferns				
Nephrolepis exaltata	0	0	30	56
Stenoloma chinensis	5	14	14	34
Sadleria cyatheoides	0	0	2	4
Pteridium aquilinum	0.4	0.4	1	4
Shrubs				
Stachytarpheta cayennensis	12	50	18	61
Psidium guajava	1	4	2	7
Lantana camara	5	11	5	14
Eugenia cumini	4	5	0	0
Melastoma malabathricum	1	1	12	25
Psidium cattleianum	1	2	0.5	1
Herbs				
Elephantopus mollis	26	63	2	5
Centella asiatica	4	36	11	56
Cassia leschenaultiana	1	16	2	34
Spathoglottis plicata	5	14	4	13
Mimosa pudica	2	6	0	0
Passiflora foetida	1	6	0.5	2
Cuphea carthagenensis	1	4	0.5	2

as *Stachytarpheta cayennensis* (joee) and *Elephantopus mollis*, a declared noxious weed (FIG. 5). Also represented in the community with a high degree of constancy are *Paspalum conjugatum*, *Centella asiatica*, *Lantana camara*, *Cassia leschenaultiana*, *Sacciolepis contracta*, and the Philippine ground orchid, *Spathoglottis plicata*. All are introduced species and of no agricultural value except for the low grazing value of the dominant grasses. The one possibly indigenous species, *Chrysopogon aciculatus* (pilipiliula), has value as a soil binder and appears on about half the plots in the association, usually on very dry, exposed, and partially eroded areas. This is considered a true pioneering species in the successional trend following disturbance.

The habitat occupied by this association is the driest of the three described, but it still receives in excess of 80 inches of precipitation

annually. It includes the ridge-top where an unimproved road was clearly marked by the growth of *Sporobolus capensis* and *Axonopus affinis* (Fig. 1), and the southwest-facing slope where the *Eugenia cumini* (Java plum) was found among the planted cultivars of *Macadamia*, *Araucaria*, and *Pandanus*. This association occupied one-half or more of the area of any given ridge in the Game Refuge.

The second association, *Setaria–Nephrolepis* (grass–fern), is slightly less extensive and occupies the northeast-facing slopes and the north sides of the ridges (Fig. 2). This area (about one-third of the total) is dominated by the same two weedy grasses: *Setaria geniculata* and *Paspalum orbiculare*. It is also well supplied with *Stachytarpheta* (Table II), *Centella*, *Cassia*, *Sacciolepis contracta*, and the *Spathoglottis*. *Paspalum conjugatum*, *Chrysopogon aciculatus*, and *Elephantopus* are much less common, but there is a substantial degree of dominance of the *Nephrolepis exaltata* and *Stenoloma chinensis*, the lace fern. The smaller Hawaiian tree fern or amaumau, *Sadleria cyatheoides*, also occurs. The noxious weedy shrub *Rhodomyrtus tomentosa* was gaining a foot-hold on this area at the time of first examination, spreading from its focus of introduction near the Kilohana Crater into favorable habitats at even greater distances. *Metrosideros* growth is vigorous in this habitat and given enough time without disturbance would eventually dominate even the *Melastoma* in most of the situations observed. Older specimens of *Metrosideros* show a marked production of aerial roots which apparently is associated with high moisture and favorable growing conditions. It should be pointed out that, in this instance, the combination of steep slope and its position athwart the northeast trade winds is thought to be responsible for the more mesic environment in this habitat type and *not*, as in more temperate climates, the protection of the north and east slopes from the effects of direct insolation, although this may play a minor role here also.

In the lower edge of this *Setaria–Nephrolepis* association there are frequent occurrences of solid stands of *Dicranopteris linearis*, the false staghorn fern (Fig. 3). *Dicranopteris* (*Gleichenia*) has been recognized as an accumulator of aluminum by several authors and has been analyzed in Hawaii (Moomaw *et al.*, 1959) where it was found to contain consistently high concentrations of aluminum. In addition to its relation to the aluminum levels in soils, *Dicranopteris* is usually associated with a mesic environment, as are most ferns. In this case the fern communities occur on the lower slopes of the ridges just above the valley-bottoms. Since free flowing water is observed in the valleys most of the year, it may be inferred that the hydrology of the area is such that the false staghorn patches coincide with the area of effluence of ground water leaching through the upper aluminous horizons. The outflow of water may not be great but it is reasonable to expect a water table not far below this level and also to expect that this percolation water is low in dissolved bases and silica and high in aluminum content. In addition, of course,

the moist drainage ways and valley bottoms are protected from the fires that have swept the ridges at frequent intervals.

The plant association in the wooded valley-bottom (FIG. 4) was not examined quantitatively as were the upper areas on the aluminous soils but a thorough reconnaissance and collection was made. This semi-riparian community is dominated at present by an overstory of *Psidium guajava* (guava) with an occasional specimen of *Pandanus odoratissimus*, *Eugenia malaccensis* (mountain apple) and *Aleurites moluccana* (candle-nut tree). The latter two species show vigorous signs of reproduction in the understory and many fallen logs indicate the former importance of these trees in the community. The trees and rocks in this moist habitat support a number of epiphytic species of lichens, mosses, liverworts, and ferns as well as climbing vascular plants. The ground cover as well, is made up of ferns in especially moist places, the dominant or frequently occurring species are *Phlebodium aureum*, *Elaphoglossum reticulatum*, *Athyrium microphyllum*, *Dryopteris dentata*, *Blechnum occidentale*, and others. The lianes include a native *Peperomia* and *Dioscorea bulbifera*. The *Zingiber zerumbet* (awa'puhi), a *Lobelia*, and *Sida acuta* occur with some regularity, and, in places where drainage is good, the ground is covered with *Oplismenus hirtellus* (basket grass) in the open shade of the dominant guava. In more moist situations, the sedges, *Cyperus alternifolius* and *Cladium meyenii*, are frequent unless completely shaded by the *Hibiscus tiliaceus* (hau tree) or unless permanent water favors a semiaquatic community with rushes, *Jussiaea suffruticosa* var. *ligustrifolia*, and *Dryopteris gongylodes*.

Effects of Fire

During the course of the studies of the Kauai bauxite area, an excellent opportunity was afforded to study the effects of fire when the Territorial Division of Fish and Game embarked on a program of burning the area adjacent to the study site in an attempt to improve the cover and food supply for game birds. Most of the area within the Game Reserve was burned over a period of months beginning in December, 1958. This was eight months after the initial vegetation examination and after eight months following the burn, a reëxamination was made of some of the same transects. The results of this detailed examination are shown in TABLE III where the kind and degree of change is shown as a "consensus" of the five transects examined.

The more marked effects of fire, eight months following the burn are the increase in some of the broad-leaved weeds, the decrease in cover of the woody plants and *Stenoloma*, and the predictable reduction in litter and organic matter on the surface of the soil (or increase in bare soil cover) (FIG. 5). Principal increasers were *Elephantopus mollis*, *Cassia leschenaultiana*, *Cuphea carthagenensis*, *Chrysopogon aciculatus*, *Emilia sonchifolia*, and *Pteridium aquilinum*. Of these, the change in *Emilia* was the most striking, since its presence was not noted at the time of the first

TABLE III. Comparative Cover of Major Species in Two Associations on Gibbsitic Soils of Kauai Before and After Fire.

SPECIES	ASSOCIATIONS					
	SETARIA–PASPALUM (3 transects)			SETARIA–NEPHROLEPIS (2 transects)		
	Before Fire		After Fire	Before Fire		After Fire
Grasses						
Setaria geniculata	78%	>	60% *	84%	>	64%
Paspalum orbiculare	27	=	32	25	=	29
Sacciolepis contracta	11	=	14	27	=	28
Chrysopogon aciculatus	9	<	20	2	=	2
Paspalum conjugatum	6	>	0.3	0	=	1
Ferns						
Nephrolepis exaltata	0	=	0	6	=	6
Stenoloma chinensis	4	>	0	2	>	0
Pteridium aquilinum	0	=	1	1	<	3
Shrubs						
Stachytarpheta cayennensis	15	=	15	24	=	26
Psidium guajava	0	=	2	4	=	4
Lantana camara	9	>	3	8	=	7
Melastoma malabathricum	4	>	0	8	>	3
Psidium cattleianum	5	>	0.1	0	=	1
Herbs						
Elephantopus mollis	32	=	31	2	=	4
Centella asiatica	3	=	5	10	=	8
Cassia leschenaultiana	1	<	5	1	<	4
Spathoglottis plicata	5	>	1	5	=	4
Passiflora foetida	1	=	1	1	=	1
Cuphea carthagenensis	0	=	1	1	<	4
Emilia sonchifolia	0	<	5	0	<	2
Bare soil	0	<	12	0	<	12

* Trends: >, decrease; <, increase; =, no change.

examination except as a casual occasional plant on disturbed areas. The increase in *Elephantopus* is not impressive, partly because of the biennial habit of the plant and partly because the change was more pronounced in the more moist *Setaria–Nephrolepis* habitat type. Not all the plants appeared to be of biennial habit since some had flowered at the time of examination. The increase of *Cassia* following fire is large and involves both numbers of plants and size of individuals. It is possible that a slight seasonal effect tends to reinforce this difference. *Cuphea* was only mildly stimulated by the burning. *Chrysopogon* has been observed to thrive on the exposed and eroded south slopes and was predictably improved in its competitive position by fire. *Passiflora foetida* increased slightly in frequency in both associations.

Species showing a strong tendency to decrease in cover or frequency following fire in the two associations studied were *Lantana camara*, *Stenoloma chinensis*, *Melastoma malabathricum* (FIG. 6), and *Paspalum conjugatum*. To a lesser degree, *Spathoglottis plicata* showed a decrease in frequency while *Setaria geniculata* declined in cover only. *Stenoloma* was completely obliterated by the fire in places where it had been recorded a year before, while the woody *Lantana* and *Melastoma* were markedly reduced in cover but observation revealed that they were by no means killed.

Species that were little affected by burning include guava, which was found only in the *Setaria–Nephrolepis* community and which was observed elsewhere to be severely damaged by fire, *Centella asiatica*, *Sacciolepis contracta*, *Paspalum orbiculare*, and *Stachytarpheta cayennensis* which increased much less than expected.

Following the simulated strip-mining and planting of the stripped area with forage, field and fruit crops, a number of species new to the area were observed. An inventory of plants new to this area and appearing in the disturbed areas was taken and these are designated as "invaders" in the APPENDIX. Since all the fruit and ornamental plants were brought in from elsewhere, some as potted plants, undoubtedly some of the invaders came in with the plants. Others such as *Solanum nigrum* (popolo) may have already been in the soil in dormant condition awaiting proper conditions before breaking their dormancy and making their appearance. Stripping, followed by field preparation, apparently supplied the necessary conditions for the germination of long dormant seeds.

SUMMARY AND CONCLUSIONS

The evidence from the present study points to conclusions similar to those from the Jamaican study of Howard and Proctor (1957) in that none of the species studied shows a definite affinity for ecologic niches characterized by high aluminum content of the soil. The species present are nearly all those adapted to a generally moist environment with warm equable temperatures, acid, infertile soils, and a shallow root zone. Since the aluminum content of the soil increases with depth while the rooting of the dominant plants is unusually shallow, it must be inferred that they are not dependent on high levels of aluminum for survival, but rather are restricted in their root development to the organic and more fertile upper horizons. In addition, the major changes in the vegetation pattern apparently are not governed by alterations in the soil profile, but rather are related to slope, exposure and effective rainfall. The high degree of disturbance of the natural pattern through fire, grazing and manipulation of the cover has further removed the expression of the natural vegetation determinants. Despite the fact that several of the species encountered are known to contain high levels of aluminum (*Dicranopteris linearis*, *Paspalum orbiculare*, *Melastoma malabathricum* and sometimes *Nephrolepis exaltata*) and are growing on

soils classed as aluminous, it can only be said that they are tolerant of the condition and are capable of accumulating the aluminum ion.

The most important single factor in the present distribution of species in the area is the locus and date of introduction of each of them and their competitive relationship both to the endemic species which they have replaced and to each other. A tabulation of the species present reveals only 5% to be endemics, while 30% are indigenous species of fairly wide Island distribution (see species list), and the remainder are introductions. The indigenous and endemic species occur more frequently in the gulch bottoms and protected areas than on the exposed and disturbed slopes and ridges, clearly indicating their remnant nature.

Other vegetation anomalies, such as the presence of *Scaevola frutescens* (beach naupaka) and other invaders, can be attributed to the importation of sand, coral and cinders at various times for road and building purposes.

Few of the species in the initial stages of succession on the Jamaican bauxites are the same as those observed on the Kauai site, but the later, more persistent weedy plants include *Lantana*, *Stachytarpheta*, and *Sida* which were present in Jamaica also. Several of the grasses used for revegetation in Jamaica are the same ones favored in the Wailua Reserve, such as *Digitaria decumbens* (Pangola grass), *Melinis minutiflora* (molasses grass), and *Panicum purpurascens* (Para grass). *Panicum maximum* (Guinea grass) was useful in the Jamaican study, while the site on Kauai was considered too wet for the successful establishment of any large-scale planting of Guinea grass. The overburden removed from the mining sites was observed to be unusually fertile in Jamaica, as it was in Hawaii, partly owing to the high content of organic matter and partly owing to the content of weed seeds, roots and living plant parts.

Studies with the major plantation and pasture crops in Hawaii have shown that successful production can be attained with applications of fertilizer in fairly large amounts. Six to eight hundred pounds per acre of complete fertilizer, with or without lime, will give good results with *Digitaria decumbens* and *Desmodium intortum* on either the mined substrate or the returned topsoil and produce a rapid vegetative cover. Sugar cane and pineapple can be grown at plantation levels of production or above, if well fertilized.

REFERENCES CITED

Braun-Blanquet, J. 1932. The study of plant communities. McGraw-Hill Book Co.

Brown, D. 1954. Methods of surveying and measuring vegetation. Comm. Bur. Past. and Field Crops Bull. **42.**

Chenery, E. M. 1948. Aluminium in the plant world. Kew Bull. **1948:** 163–173.

———. 1949. Aluminium in the plant world. *Ibid.* **1949:** 433–466.

Cline, M. G., *et al.* 1955. Soil survey of the Territory of Hawaii. U. S. D. A. Soil Survey Series 1939, No. **25.**

CROCKER, R. 1952. Soil genesis and pedogenic factors. Quart. Rev. Biol. **27**(2): 139–168.

DEGENER, O. 1932–date. Flora Hawaiiensis **1–5**. Published by the author.

HOWARD, R. A., and PROCTOR, G. R. 1957. The vegetation on bauxitic soils in Jamaica. Jour. Arnold Arb. **38**: 1–41, 151–169.

MACDONALD, G. A., DAVIS, D. A. and COX, D. C. 1954. Kauai, an ancient Hawaiian volcano. Volcano Letter No. **526**: 1–3.

MOHR, E. C. J., and VAN BAREN, F. A. 1954. Tropical soils. Interscience Publishers Inc.

MOOMAW, J. C., NAKAMURA, M. and SHERMAN, G. D. 1959. Aluminum in some Hawaiian plants. Pacific Science **13**: 335–341.

NEAL, MARIE C. 1948. In gardens of Hawaii. B. P. Bishop Museum Spec. Publ. **40**.

RIPPERTON, J. C., and HOSAKA, E. Y. 1942. Vegetation zones of Hawaii. Hawaii Agr. Exp. Sta. Bull. **89**.

SHERMAN, G. 1958. Gibbsite-rich soils of the Hawaiian Islands. Hawaii Agr. Exp. Sta. Bull. **116**.

———. and KANEHIRO, Y. 1948. The chemical composition of Hawaiian forest floors. Hawaii Agr. Exp. Sta. Bien. Rep. **1946–48**.

WEATHER BUREAU. 1959. Hawaii, annual summary, 1958. Climatological data **54**(13): 154–160.

WEBB, L. J. 1954. Aluminium accumulation in the Australian–New Guinea flora. Austr. Jour. Bot. **2**: 176–196.

EXPLANATION OF PLATES

PLATE I

FIG. 1. The *Setaria–Paspalum* association of the ridge-top, Wailua Game Refuge, Kauai. *Sporobolus capensis* is seen along the roadway. Shrubs in the background include *Eugenia cumini*, *Pandanus odoratissimus*, *Psidium guajava*, and *Melastoma malabathricum*, an aluminum accumulating species. FIG. 2. The *Setaria–Nephrolepis* association on a north-facing slope. The "Ama'uma'u" tree fern, *Sadleria cyatheoides*, is seen in the middleground. *Setaria* and *Paspalum* are the dominant grasses.

PLATE II

FIG. 3. *Dicranopteris linearis*, known to be an aluminum accumulating fern, occurs primarily on the lower slopes and valley bottoms. FIG. 4. The vegetation of the protected valleys is dominated by *Psidium guajava* and *Pandanus odoratissimus*. The understory contains high percentages of ferns (*Dryopteris*) and *Oplismenus hirtellus*, the shade-tolerant "basket grass." Most of the indigenous species were found in this association.

PLATE III

FIG. 5. A plot in the *Setaria–Paspalum* association following fire. A young orchid plant, *Spathoglottis plicata*, occurs on the left side of the plot, while the broad leaves are those of *Elephantopus mollis*. The stoloniferous grass on the bare soil is *Chrysopogon aciculatus*. FIG. 6. Regeneration of *Melastoma malabathricum* six months following fire. Top growth is completely killed back. Note that the *Setaria* has already produced mature inflorescences.

Moomaw & Takahashi, Vegetation on Gibbsitic Soils

Moomaw & Takahashi. Vegetation on Gibbsitic Soils

Moomaw & Takahashi, Vegetation on Gibbsitic Soils

APPENDIX. **Species List with Occurrence and Origin Indicated.**

Symbols: A, abundant; C, common; U, uncommon; R, rare; I, indigenous; E, endemic; *, known in Hawaii at that date; P, planted (usually by Board of Agriculture and Forestry); +, invader of stockpiled topsoil or of exposed subsoil.

SPECIES	OCCURRENCE			ORIGIN	
	RIDGE	SLOPE	VALLEY	INDIGENOUS OR ENDEMIC	INTRODUCED
FERNS AND FERN ALLIES					
Asplenium insiticium			U	?	
Athyrium microphyllum			U	?	
Blechnum occidentale			U		1923 Trop. Am.*
Cibotium chamissoi		U	U	E	
Dicranopteris linearis		C		I	
Diplazium sandwichianum			R	E	
Dryopteris dentata			C	I	
Dryopteris gongylodes			R	?	
Elaphoglossum reticulatum			U	E	
Lycopodium cernuum		U		I	
Microlepia setosa			U	I	
Microsorium scolopendria			U	?	
Nephrolepis biserrata var. *furcans*		U	U	I	
Nephrolepis exaltata	C	A	U	I	Pantropic
Nephrolepis hirsutula		R		I	
Phlebodium aureum			U		Trop. Am.
Pleuropeltis thunbergiana			U	I	
Psilotum nudum	U	U		I	
Pteridium aquilinum var. *decompositum*	U	U		I	
Sadleria cyatheoides	?	U		I	
Stenoloma chinensis	C	C		I	
GYMNOSPERMAE					
Araucariaceae					
Araucaria excelsa	U				P, Norfolk Island
MONOCOTYLEDONEAE					
Araceae					
Colocasia esculenta			U	I	
Commelinaceae					
Commelina diffusa			C		1888, Pantropic *
Cyperaceae					
Carex sp.	U			?	
Cladium meyenii			U	?	
Cyperus cylindrostachyus			U		1898, Madagascar *
Cyperus kyllingia f. *humilis*	U				1900, Pantropic *
Cyperus rotundus	C				+ 1850 *
Fimbristylis diphylla		U	U		Widespread

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	Ridge	Slope	Valley	Indigenous or Endemic	Introduced
Rhynchospora lavarum			R	E	
Scirpus validus			U		1888, N. Am.*
Dioscoreaceae					
Dioscorea bulbifera			R	I	
Gramineae					
Axonopus affinis	C	C			1912, Trop. Am.
Chloris inflata	U				+ 1906, Trop. Am.*
Chrysopogon aciculatus	U	C		I	
Coix lacryma-jobi			U		1888, Indonesia *
Cynodon dactylon	U				+ 1835, Old World *
Digitaria henryi	U				1932, Formosa
Digitaria violascens	U				+ 1917, Trop. Asia
Eleusine indica	U				+ 1840, India *
Oplismenus hirtellus			C		1841, Trop. Am.
Panicum purpurascens			U		1902, Africa
Paspalum conjugatum	C	C	C		1840, Dutch Guiana*
Paspalum orbiculare	A	A	U		1888 Asia *
Paspalum urvillei	U				1906, S. Am.
Sacciolepis contracta	C	A			+ 1906, Indonesia
Setaria geniculata	A	A			1851, Europe *
Setaria verticellata	U				+ 1860, Europe *
Sporobolus capensis	U				1903, Africa
Liliaceae					
Cordyline terminalis		U		I	
Orchidaceae					
Spathoglottis plicata	C	C			? Asia–Malaya
Pandanaceae					
Freycinetia arborea			U	E	
Pandanus odoratissimus		C	C	I	
Pandanus variegatus		U			P
Taccaceae					
Tacca leontopetaloides			U	I	
Zingiberaceae					
Zingiber zerumbet		U	U	I	India
DICOTYLEDONEAE					
Amaranthaceae					
Amaranthus hybridus	U			I	+ Pantropic
Amaranthus spinosus	U				+ 1900, Trop. Am.
Amaranthus viridus	U				+ Trop. Am.
Anacardiaceae					
Schinus terebinthifolius	U				+ 1917, S. Am.
Caryophyllaceae					
Drymaria cordata			U		1900, Asia–Malaya

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	RIDGE	SLOPE	VALLEY	INDIGENOUS OR ENDEMIC	INTRODUCED
Casuarinaceae					
Casuarina equisetifolia		U			P 1895, Malaya
Convolvulaceae					
Ipomea pes-caprae	R			I	+
Compositae					
Bidens pilosa	U				+ 1864, Trop. Am.*
Eclipta prostrata	U				Widespread
Elephantopus mollis	A	A	C		+ 1931, Trop. Am.
Emilia sonchifolia	C				+ Trop. Asia
Erechtites valerianifolia	U				+ 1870, N. Am.
Erigeron canadensis	C	R			+ ? N. Am.
Pluchea odorata	U				1931, S. Am.*
Sonchus oleraceus	U				? Europe
Vernonia cinerea	U				+ Trop. Afr., Asia
Euphorbiaceae					
Aleurites moluccana			U	I	
Euphorbia hirta	U				+ 1888, Pantropic *
Euphorbia hypericifolia	U				+ Pantropic
Euphorbia thymifolia	U				+ Widespread
Goodeniaceae					
Scaevola frutescens var. *sericea*	U	U		I	
Scaevola gaudichaudiana	U	U		I	
Lauraceae					
Cinnamomum camphora	R				? China
Leguminosae					
Albizzia moluccana		U			1917, Malaya
Cajanus cajan	U				P 1909, India
Canavalia sericea			U	I	
Cassia leschenaultiana	C	C			1888, India *
Crotalaria incana	U				+ Trop. Am.
Desmodium canum	U				P 1916, Trop. Am.*
Desmodium uncinatum	R				Trop. Am.
Mimosa pudica	C	C			1800, Trop. Am.*
Vigna marina			U		Pantropic
Lobeliaceae					
Lobelia sp.			R	E	
Lythraceae					
Cuphea carthagenensis	C				+ 1900, Trop. Am.
Malvaceae					
Hibiscus tiliaceus	U	U	C	?	?
Sida acuta		U			?
Melastomaceae					
Melastoma malabathricum	C	C			1916, India

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	Ridge	Slope	Valley	Indigenous or Endemic	Introduced
Myrtaceae					
Eugenia cumini	U	C			1866, Trop. Afr.
Eugenia malaccensis			U		
Metrosideros collina subsp. *polymorpha*	U	C		E	
Psidium cattleianum	C	U			P
Psidium cattleianum f. *lucidum*	U				1888, Trop. Am.*
Psidium guajava	C	C	A		1800, S. Am.*
Rhodomyrtus tomentosa	C	C			1920, Asia
Onagraceae					
Jussiaea suffruticosa var. *ligustrifolia*			U		1888 Pantropic *
Oxalidaceae					
Oxalis corniculatus	U				1888, N. Am.*
Passifloraceae					
Passiflora edulis	U	U	U		1880, S. Am.
Passiflora foetida var. *gossypifolia*	U	U			1888, Trop. Am.
Phytolaccaceae					
Phytolacca acinosa	U				+ Asia
Piperaceae					
Peperomia membranacea var. *waimeana*			R	E	
Portulacaceae					
Portulaca oleracea	U				+ 1888, Pantropic *
Primulaceae					
Anagallis arvensis	U				+ Europe
Proteaceae					
Grevillea robusta	U	U			Australia
Macadamia ternifolia		U			P 1890, Australia
Rubiaceae					
Richardia scabra	R				1888 Trop. Am.*
Solanaceae					
Solanum nigrum	R			?	+
Sterculiaceae					
Waltheria americana		U			1819, Trop. Am.*
Umbelliferae					
Centella asiatica	C	C			1888, Asia *
Verbenaceae					
Lantana camara	C	A	U		1858, Trop. Am.
Stachytarpheta cayennensis	A	A			Trop. Am.

NOMENCLATURAL CHANGES IN DAPHNOPSIS (THYMELAEACEAE)

LORIN I. NEVLING, JR.

TWO NOMENCLATURAL ERRORS have come to light since the publication of a revision of the genus *Daphnopsis* (Nevling, 1959). These involve (1) the illegitimacy of the subspecific name *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. and (2) the combination *Daphnopsis anomala* (HBK.) Nevl. which should have been ascribed to Domke.

The subspecific combination *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. (1959, p. 313) is an illegitimate name and must be replaced. *Daphnopsis americana*, originally described by Miller (1768) as *Laurus americana*, was based upon a Houston specimen and Houston's "Manuscript Catalogue of the Plants which he had observed growing in the islands of Jamaica and Cuba; as also at Campeachy and La Vera Cruz, in the years 1728, 1729 and 1732" (introductory comments). In the subsequent edition of the *Dictionary* (Miller, 1797), *Laurus americana* was treated as a synonym of *Daphne tinifolia* Swartz, and Miller states that it was discovered at La Vera Cruz but is also a native of Jamaica.

Swartz's name *Daphne tinifolia* (1788, p. 63) is possibly based on Miller's earlier epithet as evidenced by the inclusion of *Laurus americana* as a synonym. Swartz's publication was concerned with new species of the Antillean flora and gives the habitat only as Jamaica. There is a real question as to whether or not Swartz was aware of the occurrence of the species in Mexico, a fact which he could not know without seeing the specimen of Houston. As a result of his citation of Jamaica only, the workers postdating Swartz, having benefit of information concerning the type and type locality contained in the 9th edition of Miller's *Dictionary*, assumed that a second species quite distinct from the Mexican *D. americana* existed, even if not realized by Swartz, and treated it as such. Three combinations were made, some of them several times, involving the specific epithet *tinifolia*, and all were based on the concept that it was a distinct species restricted to various islands of the Antilles. The subspecies under consideration is restricted to Cuba, Jamaica and Hispaniola and I proposed the subspecific combination, *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. indicating the basionym of Swartz. However, the combination is illegitimate because it is based on Swartz's illegitimate name (Article 64. International Code of Botanical Nomenclature. 1956). Thus a new subspecific epithet must be chosen to replace ssp. *tinifolia*. It seems proper to choose Meissner's indefinite infraspecific epithet *cumingii* (*D. tinifolia* β. *cumingii* Meissn. [1857, p. 523]) which is based upon a staminate specimen (*Cuming 56*) now on deposit in the Naturhistorisches Museum, Wien, and place it at subspecific rank. In

addition, the names based on the Swartz basionym are transferred to ssp. *americana*. Accordingly, the nomenclature is emended to read:

Daphnopsis americana ssp. **americana**

Daphnopsis americana (Mill.) J. R. Johnston, Proc. Boston Soc. Nat. Hist. **34**: 242. May 1909; Contr. Gray Herb. ser. 2. **37**: 242. June 1909.
Laurus americana Mill. Dict. ed. 8. *Laurus* no. 10. 1768. (T.: *Houston s.n.*)
Daphne tinifolia Sw. Prodr. Veg. Ind. Occ. 63. 1788.
Daphne obovata Humb. & Bonpl. ex Wikstr. Diss. Daphne ed. 2. 40. 1820. (T.: *Humboldt & Bonpland 7549.*)
Daphne bonplandiana Kunth, Syn. Pl. **1**: 447. 1822.
Daphne lagetto Bonpl. ex Kunth, ibid. 1822, pro syn.
Nordmannia tinifolia (Sw.) Fisch. & C. A. Meyer, Ann. Sci. Nat. ser. 2. **20**: 49. February 1843; Bull. Acad. St. Pétersb. Classe Physico-Math. **1**: 355. June 1843.
Hargasseria mexicana Schiede & Deppe ex C. A. Meyer, Ann. Sci. Nat. ser. 2. **20**: 51. February 1843 (based on *Daphne bonplandiana* sensu Cham. & Schlechtd. non Kunth); Bull. Acad. St. Pétersb. Classe Physico-Math. **1**: 356. June 1843.
Hargasseria tinifolia (Sw.) Endl. Gen. Suppl. **4**^{2}: 68. 1847.
Hargasseria schiedeana Endl. ibid. 1847 (based on *Daphne bonplandiana* Kunth).
Daphnopsis bonplandii (Kunth) Meissn. DC. Prodr. **14**: 521. 1857.
Daphnopsis tinifolia (Sw.) Meissn. ibid. 523. 1857.
Daphnopsis lindenii Meissn. ibid. 1857. (T.: *Linden 95* (♀).)
Daphnopsis bonplandiana (Kunth) Standl. Contr. U.S. Natl. Herb. **23**: 1013. 1924.

Daphnopsis americana ssp. **cumingii** (Meissn.) Nevl., comb. & stat. nov.

Daphnopsis tinifolia β. cumingii Meissn. DC. Prod. **14**: 523. 1857. (T.: *Cuming 56* (♂).)
Daphnopsis americana ssp. *tinifolia* (Sw.) Nevl. Ann. Missouri Bot. Gard. **46**: 313. 1959.

An additional change involves the combination *Daphnopsis anomala* (HBK.) Nevl. (1959, p. 323). This combination was previously made by Domke and should be credited to him. *Daphnopsis anomala* (HBK.) Domke, Bibliotheca Bot. **111**: 57. 1934, in discussion.

LITERATURE CITED

Meissner, K. F. Thymelaeaceae. DC. Prodr. **14**: 493–605. 1857.
Miller, P. The Gardners Dictionary, ed. 8. 1768.
———. The Gardners Dictionary, ed. 9. 1797.
Nevling, L. I., Jr. A revision of the genus *Daphnopsis*. Ann. Missouri Bot. Gard. **46**: 257–358. 1959.
Swartz, O. Prodr. Veg. Ind. Occ. 1788.

SEEDLING LEAVES IN PALMS AND THEIR MORPHOLOGICAL SIGNIFICANCE

P. B. TOMLINSON

IN MOST PLANTS the first plumular leaves, or leaves which are produced in succession to the cotyledons, differ from normal foliage leaves in shape and size. They are referred to as "juvenile" leaves (Primärblätter of German authors) in contrast to the "adult" leaves on the older parts of the plant. Normally where adult leaves of a plant are compound or much divided the juvenile leaves are much simpler in outline. Succeeding leaves (Folgeblätter of German authors) are increasingly complex and a gradual transition from juvenile to adult foliage takes place. Exceptions to this generalization are known, as, for example, in certain members of the Quiinaceae (Foster, 1951) and *Ficus alba* (Corner, 1951; p. 681) in which adult leaves are less complex than seedling leaves.

The adult leaves of most palms are large and compound, so it is not unexpected to find that their first foliage leaves are small and usually simple. Although there is considerable variety in the shape of the first foliage leaf, it is very constant for each species and so is of considerable diagnostic importance. A practical result of this, of value to nurserymen, is that it is possible to identify, or at least find evidence of misidentification, in palms at a very early stage of growth. Unfortunately, however, records of the diagnostic characters of seedling palm leaves are not often included in taxonomic writings but they are available for *Howeia* (Cook, 1926), *Roystonea* (Cook, 1935), and *Veitchia* (Moore, 1957). The present paper describes the main shapes exhibited by juvenile palm leaves.

A second major observation is that the series of increasingly complex leaf types which occur in the transition between the first foliage leaf and later adult forms is constant and characteristic for each species. Six main series are described here, and by comparing them it is possible to arrive at certain interesting conclusions about evolutionary trends in juvenile palm foliage.

Significant correlations are also found between the type of juvenile foliage and the adult foliage in palms and it has been found possible to explain these correlations on an evolutionary basis.

There is an extensive literature dealing with the morphology and anatomy of the palm seedling (Gatin, 1912; Boyd, 1932), but, except in the writings of Micheels, Pfitzer and Drude, little attention has been paid to later stages of growth in which juvenile foliage is exhibited. Micheels (1889) and Pfitzer (1885) both emphasize the diagnostic value of seedling leaves in palms. Micheels (1889) and Drude (1889) both describe some of the series of leaves developed by young palms.

Germination of palm seeds and a new term. A brief résumé of the morphology of the palm seedling as a whole is necessary for an understanding of the observations recorded below. Excellent accounts of this subject have been written by Gatin (1906, 1912). Germination of palm seeds is hypogeal. The cotyledon is never expanded as a green, aerial photosynthetic organ because its apex remains embedded in the endosperm of the seed and becomes modified into an absorptive organ or haustorium. This converts the reserve food material of the endosperm into a soluble form. The food material is then transmitted to the rest of the embryo via a tubular "middle piece" which represents the petiole and sheath of the cotyledon. In many palms the middle piece elongates considerably and buries the seedling some distance below the seed. In other palms, in which the cotyledon does not elongate, the seedling develops next to the seed, as, for example, in the coconut.

In examining palm seedlings it must be realized that the first green leaves are not immediate post-cotyledonary leaves because one or more of the first plumular leaves are bladeless and appear as sheathing scale-leaves. Their number seems to be fixed in each species of palm. They apparently have a protective function since they envelop the subsequent bladed leaves and are therefore mechanically useful in permitting buried shoots to break through to the soil surface without damage to the enclosed foliage leaves.

The present account deals largely with the morphology of the first foliage leaves. In this account it is proposed to apply the term *eophyll* (Greek *eos*-early; *phyllon*-leaf) to the first few leaves with a green expanded lamina developed by the seedling. This term seems necessary in order to identify these organs which are only one of a series of leaf forms to which the term "juvenile" can be applied. In the present paper "eophyll" is used with reference to palms, but it may have a wider application.

OBSERVATIONS

The first eophyll of palm seedlings. In most palms the first eophyll is simple, although it may be either entire or bifid, i.e., with a deeply emarginate apex. Within these two main types there is a considerable range of form, although for a given species the shape and size is very constant. Other diagnostic eophyll features are the type and distribution of armature and indumentum. As a consequence, it is often possible to identify at least the genus to which a palm belongs from its first eophyll. In all, three main categories of eophyll may be distinguished.

Entire eophylls. These are usually linear or linear-lanceolate (Figs. 1a, 2a). Sometimes their apices are truncate as in *Corypha*, *Licuala* (Fig. 3) and *Livistona*. In the caryotoid palms *Arenga*, *Didymosperma* and *Wallichia* the first eophyll is flabellate (Fig. 4), the margin and apex being irregularly and distantly toothed.

BIFID EOPHYLLS. The depth of the apical incision varies considerably. In species of *Drymophloeus* and *Iriartea* the apical incision is so inconspicuous that the leaflet appears to be entire at a casual glance. Normally, however, the segmentation is so complete that the leaf is evidently composed of two opposite, terminal leaflets (FIGS. 7b, 8a). The apex of each segment is either acute or, as in *Hyospathe* and many of the Ptychospermate palms, truncate (FIG. 10). In *Aiphanes* the margin is irregularly toothed (FIG. 9).

COMPOUND EOPHYLLS. Many palms have a first eophyll which is always compound. This is palmate in fan-palms such as *Borassodendron*, *Latania* (FIG. 5) and *Lodoicea* but pinnate in feather-palms such as *Hedyscepe*, *Metroxylon*, *Nephrosperma*, *Phytelephas* and *Raphia*. In several genera of feather-palms certain species have simple first eophylls whilst those of other species are compound, as in *Calamus*, *Chamaedorea*, *Euterpe*, and *Howeia*. The significance of compound first eophylls is discussed later.

When the distribution of types of first eophyll throughout the whole family Palmae is considered, certain significant correlations between the shape of this organ and the morphology of the adult foliage become apparent.

Comparisons between the first eophyll and adult foliage in palms. The following arrangement of the tribes corresponds to that given by Drude (1889).

A. INDUPLICATE PALMS (segments V-shaped in section).

Phoeniceae: Adult leaves imparipinnate, terminal leaflet always distinct; first eophyll entire, lanceolate.

Sabaleae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate, apex truncate in *Corypha*, *Licuala* and *Livistona*.

Borasseae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate but with a truncate apex in *Borassus* and *Hyphaene*; digitately compound in *Borassodendron*, *Latania* and *Lodoicea*.

Caryoteae excluding *Caryota*: Adult leaves imparipinnate, terminal leaflet often inconspicuous; first eophyll entire, somewhat flabellate.

Caryota: Adult leaves bipinnate; first eophyll bifid.

B. REDUPLICATE PALMS (segments Λ-shaped in section).

Lepidocaryineae: Adult leaves mostly paripinnate, pair of terminal leaflets often obscure; costapalmate in *Lepidocaryum* and *Mauritia*; first eophyll usually bifid, but pinnately compound in *Metroxylon*, *Raphia* and species of *Calamus* and *Daemonorops*.

Areceae and Geonomeae: Adult leaves mostly paripinnate, terminal pair of leaflets usually conspicuous and equal, rarely adult leaves persistently bifid as in species of *Geonoma*, *Hyospathe* and *Reinhardtia*; first eophyll mostly bifid, but pinnately compound in species of *Acanthophoenix*, *Euterpe*, *Hedyscepe*, *Howeia* and *Nephrosperma*, and entire, lanceolate in *Roystonea* and *Stevensonia*.

Iriarteae: Adult leaves paripinnate, terminal pair of leaflets usually conspicuous and equal, apices of segments usually irregularly toothed; first eophyll bifid, almost entire in *Iriartea* because of a very shallow apical incision; entire and lanceolate in the anomalous genus *Ceroxylon*.

Morenieae: Adult leaves usually paripinnate, adult leaves persistently bifid in some *Chamaedorea* species; first eophyll usually bifid, rarely pinnately compound in some species of *Chamaedorea*; entire and lanceolate in the anomalous genus *Pseudophoenix*.

Attaleae and Elaeideae: Adult leaves irregularly pinnate, terminal leaflets arranged irregularly, often obscure; first eophyll entire, lanceolate, but bifid in *Cocos nucifera*.

Bactrideae: Adult leaves paripinnate, terminal leaflets conspicuous and equal; rarely adult leaves persistently bifid in species of *Astrocaryum* and *Bactris*; first eophyll always bifid.

Phytelephas and *Nypa*: Adult leaves pinnate; first eophyll in *Phytelephas* pinnately compound. The morphology of the seedlings in these two genera is not well understood and they are not considered further in this account.

It may be noted that the first leaves of basal suckers of caespitose palms are usually simple, i.e., they revert to the juvenile condition.

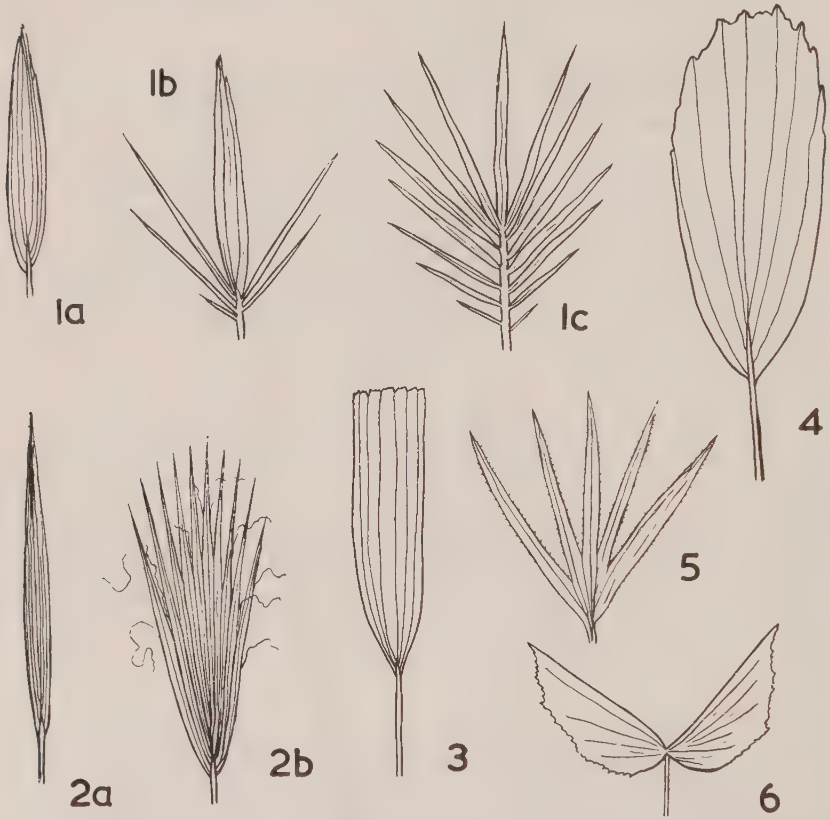
Transitions to the adult foliage. In most palm seedlings, after one or more leaves of the same shape as the first eophyll have been produced, a long series of transitional leaves of increasing complexity is developed until the type of foliage characteristic of the adult plant appears. Although each species of palm produces its own characteristic series of transitional leaves, six main classes can be recognized. These are described below in relation to both the first eophyll and the adult type of leaf.

A. Induplicate palms.

Class 1. *First eophyll entire; adult foliage leaves imparipinnate* (Figs. 1a–c). The eophylls (Fig. 1a) are succeeded by imparipinnate leaves of increasing size in which the odd terminal leaflet resembles the whole lamina of the first eophyll (Figs. 1b, c). This type occurs in *Phoenix* and in all the Caryotoid palms except *Caryota*. In *Phoenix* the odd terminal leaflet can always be recognized in undamaged adult leaves but often in the Caryoteae the situation is less regular so that the imparipinnate condition is only clear in small transitional leaves.

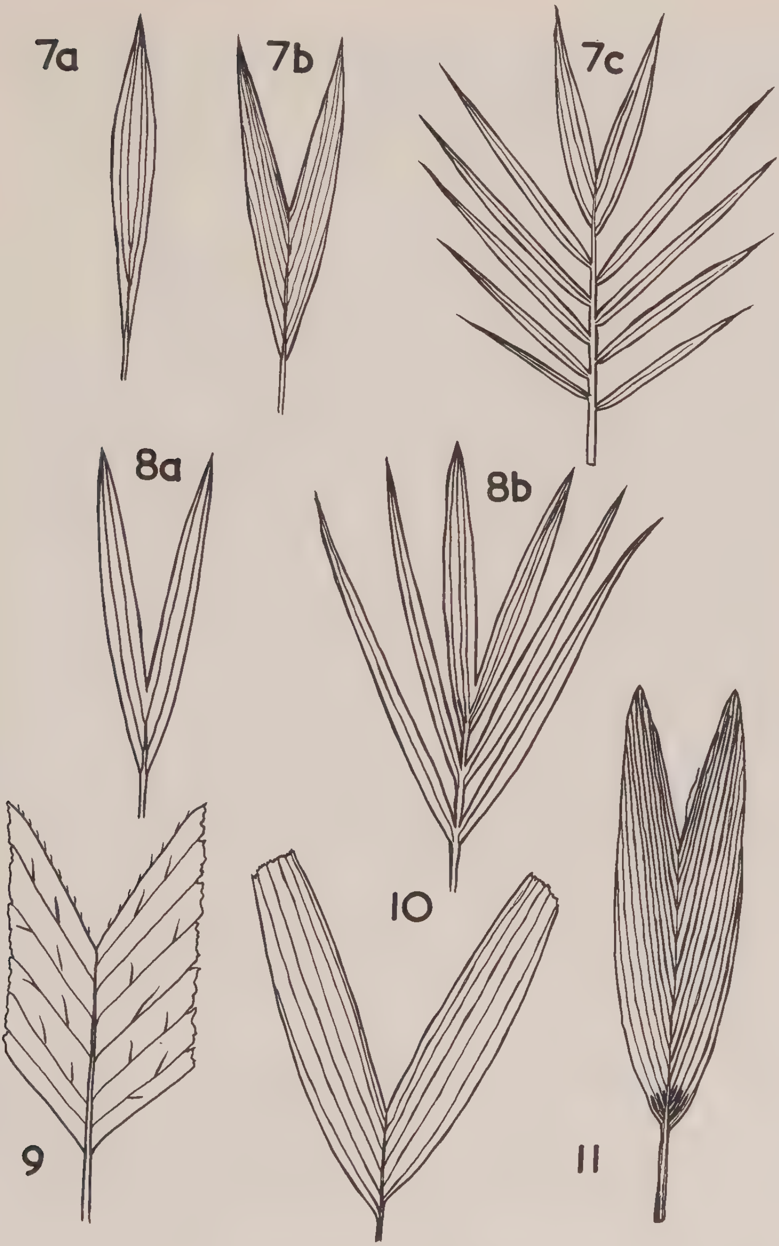
Class 2. *First eophyll entire; adult foliage leaves palmate or costapalmate* (Figs. 2a, b). This class is confined to the fan-leaved tribes Sabaleae and Borasseae. The first, linear foliage leaves (Fig. 2a) are followed by broader leaves in which the lamina is incompletely split into a number of narrow segments (Fig. 2b). Later leaves are broader still and with more segments as the adult foliage is gradually approached. Normally the segmentation of these transitional leaves is not symmetrical, although

rarely an odd terminal segment can be recognized, as in *Coccothrinax*, *Livistona* and *Trachycarpus*. In *Cryosophila* and *Sabal* the transitional leaves are often bifid as a result of a deep median split. This split persists in mature leaves of *Cryosophila*, the blades of which consequently have equally segmented halves. In all fan palms it is assumed that the terminal leaflet has been displaced.



FIGS. 1–6. Lamina of eophylls in induplicate-leaved palms. 1, *Phoenix pumila*: a, first eophyll, b, c, succeeding transitional eophylls. 2, *Washingtonia filifera*: a, first eophyll, b, transitional juvenile leaf. 3, *Licuala peltata*, first eophyll. 4, *Arenga pinnata*, first eophyll. 5, *Latania sp.*, first eophyll. 6, *Caryota urens*, first eophyll.

Caryota. First eophyll bifid; adult foliage leaves bipinnate. This type is anomalous. In the adult foliage the primary rachis ends in a pair of leaflets comparable to the bifid lamina of the first eophyll (FIG. 6). The transition series between juvenile and adult foliage is long and complex. Some of the intermediate stages in which the leaves are once-pinnate with basal leaflets tending to become secondarily segmented resemble the adult foliage of species of *Didymosperma* and *Wallichia*.



FIGS. 7–11. Lamina of eophylls in reduplicate-leaved palms. 7, *Roystonea regia*: a, first eophyll, b, c, succeeding transitional juvenile leaves. 8, *Chrysalidocarpus lutescens*: a, first eophyll, b, transitional juvenile leaf. 9, *Aiphanes* sp., first eophyll. 10, *Ptychosperma macarthurii*, eophyll. 11, *Cocos nucifera*, eophyll with basal perforations.

B. REDUPLICATE PALMS.

CLASS 3. *First eophyll entire; adult foliage leaves paripinnate* (FIGS. 7a–c). The first lanceolate eophylls (FIG. 7a) are succeeded by bifid eophylls (FIG. 7b) and then by paripinnate compound leaves of successively larger size (FIG. 7c). This transition series is the longest exhibited by reduplicate-leaved palms since it includes all possible types of first eophyll which they are capable of producing. It is known only in *Roystonea* and *Stevensonia.*

CLASS 4. *First eophyll bifid; adult foliage leaves paripinnate* (FIGS. 8a, b). The bifid eophylls (FIG. 8a) are eventually succeeded by pinnate leaves bearing a pair of terminal leaflets which resemble the whole lamina of the first eophyll (FIG. 8b). This last may be striking in palms in which the terminal leaflets are broader than the remaining leaflets. Sometimes, however, the arrangement of distal leaflets in the adult foliage is not regular and the adult foliage leaf is then not obviously paripinnate. This series corresponds to the previous one but for the omission of the initial lanceolate eophyll. It is found in the majority of palms belonging to the tribes Areceae, Bactrideae, Iriarteae, Lepidocaryineae and Morenieae together with *Cocos* of the Attaleae.

CLASS 5. *First eophyll entire; adult foliage irregularly pinnate.* In this class there is great variation in the shape of transitional leaves within a single species and even within a single individual. It is impossible to describe the juvenile leaves as either paripinnate or imparipinnate since they are not segmented regularly. Often the later eophylls have incomplete splits so that the blade is irregularly fenestrate. Other examples are common in which one half of the blade is entire whilst the other is partly or wholly segmented. The same irregularity and obscurity characterizes the terminal segments of adult leaves because the most distal leaflets are often filamentous and difficult to distinguish from the filament which terminates the rachis. This class characterizes most members of the Elaeideae and Attaleae and probably also occurs in *Ceroxylon* and *Pseudophoenix. Cocos*, together with other rare exceptions from the above mentioned tribes (e.g., *Attalea allenii*), has uniform paripinnate leaves and exhibits the series of Class 4.

C. MIXED REDUPLICATE AND INDUPLICATE PALMS.

CLASS 6. *First eophyll compound; adult foliage leaves either pinnate or palmate.* The occasional and mostly unrelated genera in which the first eophyll is compound have a transitional series which includes no new leaf forms, there being merely an increase in size until the adult type of foliage is produced.

DISCUSSION

A fairly constant correlation between the shape of the first eophyll and the morphology of the adult foliage is apparent in the information presented above. It is that the induplicate (V-folded) palms normally

have an entire, lanceolate first eophyll and that the adult leaf is imparipinnate. On the other hand the reduplicate (Λ-folded) palms normally have a bifid first eophyll and an adult leaf which is paripinnate, whereever this condition can be recognized with certainty. It is suggested below how this correlation could arise and also how to account for apparent exceptions.

From the above it might also appear that there is a primary connection between fan-leaves and an entire first eophyll. However, it is generally regarded (see Eames, 1953) that the palmate leaf is merely a pinnate leaf with a condensed rachis or, more precisely, is equivalent to a pinnate leaf in which the rachis fails partly or wholly to elongate. It so happens that this trend has occurred mainly in the induplicate-leaved palms so that the two major tribes of this group, the Sabaleae and Borasseae, are entirely palmate. On the other hand only *Lepidocaryum* and *Mauritia* of the reduplicate-leaved group have developed palmate leaves.

Although palmate leaves of the borassoid and sabaloid tribes are thus morphologically equivalent to imparipinnate leaves, the development of an odd terminal leaflet, even in juvenile foliage or in costapalmate leaves which have a short but distinct rachis, is infrequent. In these palms it is assumed that the terminal leaflet has been displaced.

Before these correlations can be satisfactorily explained it is first necessary to account for the variation in eophyll morphology.

Phylogenetic trends in eophyll shape. The considerable range of eophyll shape and type in transitional juvenile foliage in palm seedlings (see FIG. 12) seems to result from certain evolutionary trends. It is assumed that a long and gradual transition between the first eophyll and the adult foliage leaf, including an extensive series of intermediate forms, is a primitive one, and that in more recently evolved palms one or more of the members of this series is omitted during seedling development. Essentially the same suggestion has been made by Dufour (1910) for some members of the Ranunculaceae in a paper describing juvenile foliage in *Anemone* and *Ranunculus* which was brought to my attention during the preparation of this article. The situation is somewhat complicated in palms because two main series of leaves are present: those with reduplicate and those with induplicate vernation. Parallel evolutionary trends have occurred independently within each series, and most possible stages of eophyll elimination occur.

REDUPLICATE PALMS. The longest series of different eophyll forms in this group are those exhibited by *Roystonea* and *Stevensonia* which form Class 3 (FIG. 12, lower left). This is assumed to be the primitive condition. The large Class 4 to which most reduplicate palms belong has been derived by omission of the initial entire eophyll (FIG. 12, lower middle left). In Class 6 are found those species in which both simple types of eophyll are omitted so that the first foliage leaf is pinnately compound (FIG. 12, upper middle left). This represents the most advanced condi-

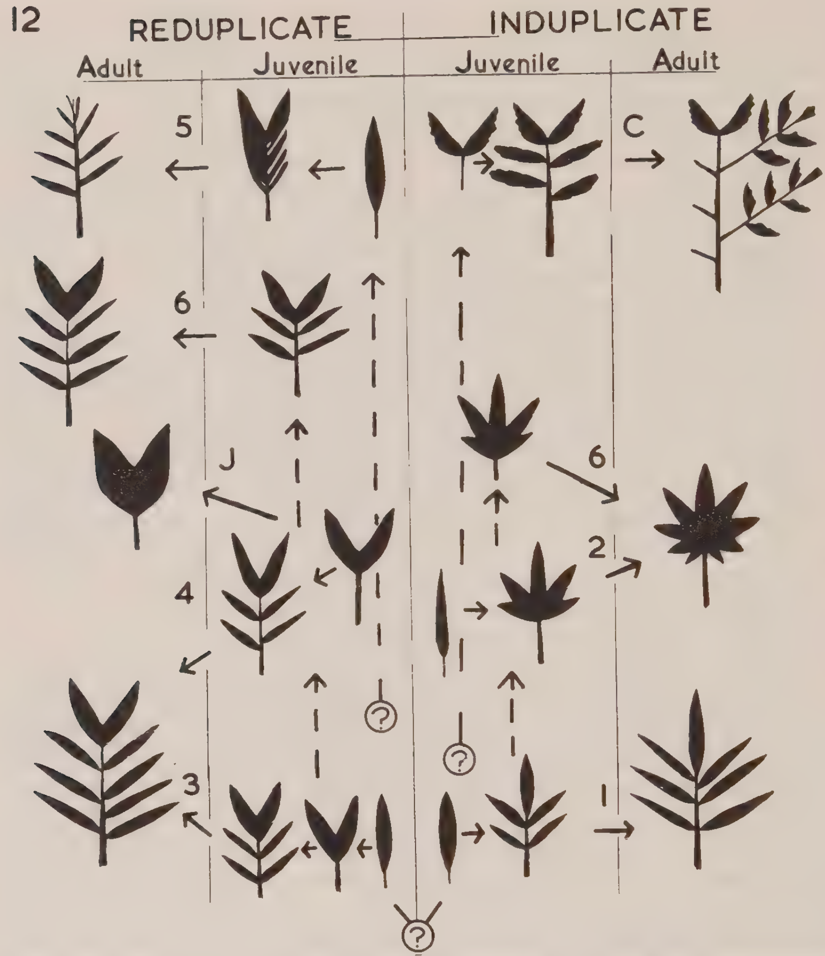


FIG. 12. Diagrammatic representation of blade shape in adult and juvenile palm leaves. Further explanation in text. Solid arrows indicate ontogenetic series. Broken arrows indicate presumed phylogenetic series. Numbers refer to classes described in text.

tion. It is evidently a derived and not a primitive condition since it has appeared quite independently in unrelated genera.

The cocoid palms of Class 5 (FIG. 12, upper left) are anomalous. The first eophyll is entire and certainly represents a primitive condition but the subsequent irregularly pinnate transitional leaves which are characteristic of this class indicate a special evolutionary trend. A possible explanation of this trend is given below.

INDUPLICATE PALMS. Class 1, exemplified by *Phoenix* represents the primitive condition in this group (FIG. 12, lower right). Since only two types of eophyll are present, only one derivative type is possible. This

is found in the three borassoid genera in which the initial entire eophyll is omitted so that the first eophyll is palmately compound (FIG. 12, upper middle right). None of the sabaloid palms show this advanced condition. One other possibility has never been realized because none of the pinnate induplicate palms possess a pinnately compound first eophyll.

Caryota is obviously a derived type although it is difficult to account for its bifid first eophyll, a type of leaf not otherwise found in the induplicate palms (FIG. 12c, upper right). This genus merits a detailed developmental study.

Permanent juvenile foliage. In the evolutionary trend described above, certain types of juvenile foliage are omitted from the ontogenetic series. The converse trend, in which the adult type of foliage is never produced, is common, usually being found in palms with a reduced habit in which the stems are short and the internodes narrow. In these palms the juvenile foliage persists throughout the life of the plant (FIG. 12j, upper middle left), or at the most compound leaves with very few segments are produced. This feature has had a polyphyletic origin since it is exhibited by several unrelated genera.

Amongst the fan palms some species of *Licuala* and *Teysmannia* have an undivided, orbicular lamina, or at the most segmentation consists of shallow marginal incisions. In the feather palms more obvious juvenile foliage is retained in several species of the genera *Astrocaryum*, *Chamaedorea* and *Geonoma*. In these species the simple foliage leaves resemble the first eophylls of related species with reduplicately pinnate adult foliage. In *Bactris militaris*, *B. wendlandiana*, and *Hyospathe concinna* the leaves are always simple, unlike the pinnate adult leaves of the remaining species in these genera. Normally these persistent juvenile leaves are small, although in *Bactris militaris* the undivided leaves may be ten feet long.

The genus *Reinhardtia* is of special interest. *Reinhardtia elegans* has pinnate leaves and is considered by Moore (1957) to be the most primitive member of the genus. Other species are smaller and have fewer leaflets. *Reinhardtia latisecta* and varieties of *R. gracilis* have either simple leaves or at the most leaves with two or three segments. An additional peculiarity in these last two species is the presence of small perforations at the base of the lamina, close to its insertion on the rachis. These perforations are evidently incomplete splits. Somewhat homologous "fenestrate" leaves occur among the juvenile foliage of many cocoid palms and they are particularly striking in seedling coconuts (FIG. 11). Evidently it is common for *Reinhardtia* to have persistent juvenile foliage.

The general conclusion is that where simple leaves characterize the adult foliage of palms, they represent a derived and not a primitive condition.

Possible origin of the palm leaf. On the basis of his studies on the development of the palm leaf, Eames (1953) makes the following state-

ment: "The compound leaf of the palm has been derived from the simple leaf by the dissection of the blade into leaflets attached to a rachis which represents the midvein of the ancestral leaf. The number and form of the leaflets are controlled by the venation pattern of the ancestral simple leaf." It is doubtful, as has just been shown, that any of the simple leaves in existing palms represent this ancestral type. The only primitive simple leaf in palms is the lanceolate first eophyll of *Phoenix* and *Roystonea*. However, it would be unwise to compare this juvenile leaf with archaic adult forms, although it is very probable that the ancestors of existing palms had a first eophyll essentially the same as that in *Phoenix* and *Roystonea*.

On the other hand, it is possible to construct mentally an ancestral palm leaf from which all existing leaf types can be derived by the splitting processes described by Eames. This archetype leaf would have a regularly plicate, entire lamina, with numerous lateral major veins in the form of ribs occupying the dorsal and ventral crests of the folds. Each vein would have a somewhat sigmoid course, its end in the leaf margin either passing to the apex or fusing with the ends of lower veins to form a marginal commissure. The thickened midrib would extend to the apex of the leaf and there become an abaxial rib (FIG. 13a). This is essentially the type of leaf envisaged by Eames. The nearest approach to it in living palms is found in such genera as *Manicaria, Mascarena, Stevensonia*, and *Vershaffeltia* in which the congested leaflets often are persistently coherent along the margins. From a distance leaves of these genera appear to be entire.

It is appropriate to mention at this point that the leaf of a fossil plant (*Sanmiguelia lewisii* Brown) has recently been described and interpreted as that of a primitive palm (Brown, 1956). Whilst this leaf does not bear all the essential features listed above, the chief difference being the absence of a midrib, it could still serve as a fundamental type from which modern compound palm leaves have evolved by the methods suggested below. The age of this plant is also noteworthy since, if it is interpreted correctly, it would be the remains of the earliest known flowering plant.

The splitting which produces individual segments may occur in three possible ways. First, the leaf may split along the ventral (abaxial) crests of the folds (FIG. 13b). This would produce reduplicate segments. At the leaf apex there could be either two equivalent splits, one on each side of the rachis, or a single split could bisect the rachis. In both examples a pair of equal terminal leaflets would result, but in the former type of splitting the free end of the rachis would persist as a whip-like filament, a feature not uncommon in paripinnate palms but particularly prominent in *Cocos* (Venkatanaryana, 1957). This situation accounts satisfactorily for the paripinnate, reduplicate leaf but it will only arise if there is a regular arrangement of ribs at the leaf apex. In contrast the cocoid palms of class 5 apparently owe their irregularly pinnate leaf to the fact that the ribs, at least at the leaf apex, are not equally spaced and that splitting is not regular. The segments here are reduplicate and the leaf is essentially

paripinnate as is revealed by the few rare examples in which the arrangement of distal leaflets is regular.

The second possibility is that the splits which separate adjacent segments take place along the dorsal (adaxial) crests (FIG. 13c). This produces induplicate leaf segments and an odd terminal leaflet so that the leaf is automatically imparipinnate. This is the type of leaf found in *Phoenix* and the Caryoteae. The palmate leaf of the Borasseae and Sabaleae is a similar leaf with a partly or wholly condensed rachis in which it is assumed that the terminal leaflet is normally displaced and is no longer recognisable.

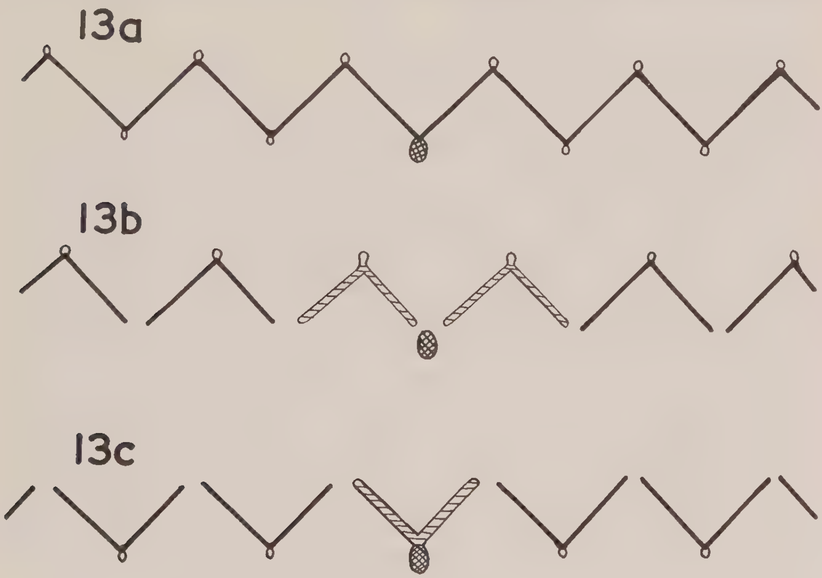


FIG. 13. Suggested origin of reduplicate and induplicate leaves from a hypothetical unsegmented ancestral leaf. a, Diagrammatic transverse section through apex of ancestral leaf with plicate but unsegmented lamina. b, Origin of reduplicate segments by cleavage along ventral crests. c, Origin of induplicate segments by splitting along dorsal crests. Rachis crosshatched, terminal segments lined. Splits are assumed to eliminate the ribs, otherwise the ribs themselves could be divided and the segments would then have marginal half-ribs.

The third possibility is for splits to occur without reference to the folds. This condition is known only in the small fan palm *Rhapis* which as a consequence has unequal and irregular segments (Naumann, 1887).

Although this theory accounts for the correlation between leaf shape and vernation it is an over-simplification of the situation. Eames, in confirmation of the observations of several early workers has clearly shown that the plication of palm leaves is a result, not of simple folding, but of a cleavage and invagination of a solid tissue.

This process is completed before the leaf primordium is more than a few millimeters high and results in a plicate blade, the margin of which is con-

nected by a continuous strip of tissue. The splitting that results in the separation of adjacent segments occurs later and, according to Naumann, may take place in a variety of ways. However, this complex developmental process does not invalidate the above argument, since it is possible that the primitive palm leaf developed an entire, plicate lamina by the same initial cleavage process. On the other hand, the view of Arber (1922) that the palm leaf is a modified phyllode may mean that at no stage in its phyletic history was there an entire unsegmented blade.

The diagram constructed by Eames (1953, FIG. 11), based on *Roystonea*, showing the origin of equally-spaced folds in the leaf primordia will only result in mature leaves in which the segments are equal, uniformly spaced and either opposite or regularly alternate on the two sides of the rachis. This regularity is relatively uncommon in palms. Many palm leaves may be described as irregularly pinnate (since the leaflets are not evenly spaced) or unequally segmented (since the leaflets are not all of the same width) and combinations of these two types are common (Tomlinson, 1961). In irregularly pinnate leaves the initial clefts must be irregularly spaced in the primordium. The most difficult situation to account for is one in which the pinnae are fasciculate, individual clusters being separated by long, naked portions of the rachis, and in which clusters of leaflets are subopposite or even alternate. It is easier to account for unequally segmented leaves which evidently arise because splits separating individual segments occur at irregular intervals and along only a few furrows. Even so, the enormous range in the morphology of individual leaflets has still to be accounted for and only detailed studies of the development of the more outstanding leaf forms will reveal the mechanism of their origin. It is clear, on the other hand, that the fundamental process described by Eames takes place in the early stages of development of all adult palm leaves. The palms are undoubtedly an ancient group with a long phylogenetic history so it would not be unexpected to find minor divergence from the fundamental mechanism of leaf development inherited from primitive forms. Much of the controversy which exists in the literature dealing with the development of the leaf in palms is likely to be a consequence of this diversity.

Morphogenetic considerations.

From the account given by Eames it is apparent that three essential processes are responsible for the development of the palm leaf:— (i) a cleavage and folding of solid tissue during very early stages of leaf ontogeny, (ii) elongation of the rachis to a greater or lesser extent during the later stages, (iii) a splitting whereby adjacent leaf segments become free. The vast range of leaf forms in palms is a result of variation in the intensity of these processes. Consequently, if any one of them could be influenced experimentally it should be possible to modify the final leaf shape. Leaves vary considerably in the extent to which external influences modify their ultimate shape (Ashby, 1948) but the susceptibility of the palm leaf to

changes in environmental conditions has never been explored. There are obvious technical difficulties involved in using palms as experimental objects. However, this account has shown that the essential morphology of the palm leaf is established very early during the production of juvenile foliage and therefore the possibility of carrying out experiments on palm seedlings grown in greenhouses in a cool temperate climate is not excluded.

One suggested experiment would be to establish whether failure of the rachis to elongate in typical palmate leaves is the result of an inhibition process which could be overcome by application of growth substances and, if so, whether it would be possible to recreate a presumed ancestral leaf.

SUMMARY

In the development of the palm seedling there is a gradual transition from small, usually simple leaves to the large compound leaves of the adult foliage. It is suggested that in the evolution of palms, one or more of the simple types of leaf which were present in the transitional series in the primitive palm and which are still extant in *Phoenix* and *Roystonea*, have been omitted and so the different types of transition series in existing palms produced. The most highly evolved seedlings have a compound first foliage leaf. A reverse trend is one in which the juvenile foliage persists and is present throughout the life of the palm.

There is found to be a significant correlation between (a) the shape of the first foliage leaf (first eophyll), (b) the series of transition forms between juvenile and adult foliage, (c) the morphology of the adult leaf, (d) the type of folding in the individual leaf segments. Palmate leaves are not essentially different from pinnate leaves. Two main groups exist in palms, the induplicate-leaved palms being imparipinnate, the reduplicate palms being paripinnate. It is suggested that these two forms are a result of a simple difference in the way in which a hypothetical entire, plicately-folded prototype palm leaf has been segmented.

The great variety in the morphology of adult palm leaves can be accounted for on the basis of variation in three fundamental processes which occur during their development. It is possible that these processes can be influenced artificially.

The present article is partly the outcome of several long discussions with Dr. H. E. Moore, of the Bailey Hortorium, Cornell University. I should like to thank him for clarifying many details and for correcting me on many points.

BIBLIOGRAPHY

ARBER, AGNES. On the development and morphology of the leaves of palms. Proc. Roy. Soc. London. B. **93:** 249–261. 1922.

ASHBY, E. Studies on the morphogenesis of leaves. I. An essay on leaf shape. New Phytol. **47:** 153–176. 1948.

Boyd, Lucy. Monocotylous seedlings. Trans. Bot. Soc. Edinburgh **31**: 1–224. 1932.

Brown, R. W. Palmlike plants from the Dolores Formation (Triassic), S. W. Colorado. U. S. Geol. Surv. Prof. Paper **274H**: 205–209. 1956.

Cook, O. F. A new genus of palms based on *Kentia forsteriana*. Jour. Wash. Acad. Sci. **16**: 392–397. 1926.

———. Juvenile characters of royal palms. Science **81**: 590. 1935.

Corner, E. J. H. Wayside trees of Malaya. ed. 2. vol. **1**. 1951.

Drude, O. Palmae. *In* Engler and Prantl, Die natürlichen Pflanzenfamilien II. 3: 1–93. 1889.

Dufour, L. Études des feuilles primordiales de quelques plantes. Rev. Gén. Bot. **22**: 367–384. 1910.

Eames, A. J. Neglected morphology of the palm leaf. Phytomorphology **3**: 172–189. 1953.

Foster, A. S. Heterophylly and foliar venation in *Lacunaria*. Bull. Torrey Bot. Club **78**: 382–400. 1951.

Gatin, C. L. Récherches anatomiques et chimiques sur la germination des palmiers. Ann. Sc. Nat. Bot. IX. **3**: 191–314. 1906.

———. Les palmiers: histoires naturelles et horticoles des different genres. Paris. 1912.

Micheels, H. Récherches sur les jeune palmiers. Mém. Cour. Acad. R. Belg. **55**: 1–126. 1889.

Moore, H. E. Synopses of various genera of Arecoideae. Art. 21. *Veitchia*; Art. 23. *Reinhardtia*. Gent. Herb. **8**: 481–536, 541–576. 1957.

Naumann, A. Beiträge zur Entwicklungsgeschichte der Palmenblätter. Flora **70**: 193–253. 1887.

Pfitzer, E. Ueber Fruchte, Keimung und Jugendzustände einiger Palmen. Ber. Deutsch. Bot. Ges. **3**: 32–52. 1885.

Tomlinson, P. B. Anatomy of the Monocotyledons. Vol. **2**. Palmae. 1961 (*In press*).

Venkatanaryana, G. On certain aspects of the development of the leaf of *Cocos nucifera* L. Phytomorphology **7**: 297–305. 1957.

Department of Botany
University of Leeds

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1960

The Staff:

It is with regret that the sudden death of Dr. Ivan M. Johnston on May 31, 1960, is recorded. Dr. Johnston, Associate Professor of Botany and a member of the staff of the Arnold Arboretum since 1931, was known in the botanical world for his monographic studies on the Boraginaceae and for his floristic work in the deserts of the United States, Mexico and South America. A biographical report of his life and professional career, as well as a bibliography of his published works, will appear in the next number of the *Journal of the Arnold Arboretum.*

Dr. Karl Sax, Professor of Botany, retired on August 30, 1959 and has served as Visiting Professor of Botany at the Gibbs Research Laboratory, Yale University, for the remainder of the year.

Three staff resignations also were accepted. Dr. Frances M. Jarrett, Botanist, resigned October 31st to accept a post at the Royal Botanic Gardens, Kew, England. Mrs. Claude Weber, Botanist, resigned September 1st to enter the graduate school of Radcliffe College. Mrs. Mary Lehmer, Business Secretary, resigned June 15th and will live in Albuquerque, New Mexico. Each contributed devoted and valuable services to the Arnold Arboretum and each carries with her our appreciation.

Two new scientists were appointed to the staff. Dr. Lorin I. Nevling was appointed Assistant Curator, beginning October 15. Dr. Nevling, who received his Ph.D. degree from Washington University in St. Louis, has been working on the Thymelaeaceae of the New World. Dr. Joab L. Thomas, a graduate of Harvard University, was appointed Cytotaxonomist as of July 1. Dr. Thomas, whose doctoral thesis dealt with the Cyrillaceae, will work primarily on the cytology and genetics of the cultivated plants in the living collections of the Arboretum.

During the year Mr. Henry Draper was appointed Superintendent of the Case Estates at Weston, Miss Ann Waterman was appointed jointly with the Gray Herbarium as Assistant Librarian, and Miss Ann Close became Business Secretary.

The Ninth International Botanical Congress was held in Montreal, Canada, between August 19th and 29th, 1959. Approximately three thousand botanists, representing many fields of research, plus wives and children attended these meetings. We were pleased that approximately 100 foreign scientists visited the combined herbaria and the living collections before, during and after the meetings. Eleven members of the Arboretum staff attended the pre-congress nomenclatural meetings. During the congress Dr. Howard presented an invitational paper titled "The Vascular

Anatomy of the Petiole as a Taxonomic Character" at a symposium on plant anatomy. Dr. Hu reported on "The Taxonomy, Geography and Economic Importance of the Genus *Fraxinus* in China" at a session on plant taxonomy. Dr. Wood was appointed to the Subcommittee for Family Names of the Committee for Spermatophytes. Dr. Howard was elected President and Dr. Wagenknecht, Secretary of the International Association of Botanical Gardens, both to serve for five years.

The annual meeting of the American Association of Botanical Gardens and Arboreta, held in conjunction with that of the American Horticultural Council at Rochester, New York, in October, was attended by Drs. Howard, Wagenknecht and Wyman. Following this meeting Dr. Wyman was appointed chairman of the committee on Plant Registration for the Association.

The Arboretum staff was represented at the annual meeting of the Plant Propagators Society by Mr. Fordham. The staff again made the necessary arrangements for the annual meeting of the New England section of the American Society of Horticultural Sciences which was held in Cambridge. Five staff members attended these meetings with three presenting technical papers. Dr. Howard was a participant in the Tropical Botany Conference sponsored jointly by the National Academy of Science and the National Research Council and held at the Fairchild Tropical Garden, May 5–7, 1960.

During the year the combination of the American Horticultural Society and the American Horticultural Council was effected. Dr. Wyman served for five years as Secretary of the latter organization which maintained its business office at the Arnold Arboretum. Following the union of the two groups as the American Horticultural Society, Dr. Wyman resigned as Secretary of the Council and was then elected First Vice-President of the new society, the headquarters of which will be in Washington, D. C.

Awards of recognition came to Drs. Wyman and Sax during the year. A special award to a professional horticulturist for outstanding accomplishments and contributions was given to Dr. Wyman by the Horticultural Society of New York. Dr. Sax received the Jackson Dawson Medal from the Massachusetts Horticultural Society and was named "Horticulturist of the Year" at the University of Massachusetts students' horticultural show.

Horticulture:

The winter of 1959–60 was unusually mild with only a single heavy snowfall. These conditions allowed for nearly continuous out-of-door work in the cleaning of many shrub plantings and in the pruning and removal of dangerous trees. Much of this work was necessitated by the extreme weather conditions of the previous year. The effects of the severe winter of 1958–59 became more evident in many plants as the season progressed and were again visible in the spring of 1960. The most conspicuous damage occurred on some, but not all, plants of the hardy strain of *Albizzia julibrissin* var. *rosea.*

The Arnold Arboretum in June, 1960. ABOVE: Bussey Brook as it flows through the *Rhododendron* collection. BELOW: A view across the lilac collection toward the torch azaleas in the oak woods.

The spring season of 1960 appeared to be a short one. It was not possible to complete all the transplanting from the nursery in Weston to the permanent plantings in Jamaica Plain, but 214 species, varieties and

cultivars were moved. Some of these were used to augment existing group plantings and others replaced weak or poorly grown plants. Many were new, representing additions to the permanent plantings.

Several plantings received special attention during the year. The collection of tree peonies, moved the previous year, is being pampered until it is well established in its new area. Approximately 1700 bulbs of *Narcissus* cultivars were added to the naturalized area being created along Bussey Brook. The mass planting of torch azaleas along the South Street bank was pruned, cleared and fertilized. The *Taxus* and *Juniperus* collections which had become crowded during recent years were given special attention, several of the large yews and junipers were moved, and some duplicate plants taken out. New specimens have been added to the main collection and the general appearance is much improved with favorable growth conditions again present in the area.

The city of Boston through its Department of Parks and Recreation continued the annual program of improvement of the roads, paths and benches which is its responsibility. A new surface was placed on the full extent of the road between South Street and Bussey Street in the area of the *Rhododendron* and conifer collections. The meadow road from the Arborway passing in front of the administration building to the maple collection was also resurfaced. These two areas not only represented the most serious deterioration of the roadways, outside of the Peters Hill area, but were also the sections most heavily travelled by visitors and by Arboretum equipment. It is hoped that additional areas may be resurfaced as city funds permit. The Department of Parks and Recreation also completed the last portion of the work of clearing the cobblestone gutters within the Arboretum. The area of Peters Hill is now clear and the whole roadway much improved. The dirt which had accumulated in the gutters had become overgrown and was salvaged for fill. Chemical sprays are now used to keep the cobblestones free of weeds.

During the year Mr. Williams, the superintendent, worked out a simple system of spraying with "Dowpon" to edge sharply and effectively the many plantings and beds in the shrub collection. Experiments continue on chemical methods of weed control as a means of improving the appearance of the grounds and of reducing the amount of hand labor required. This experimental program involves the type of chemical, the rate and frequency of application. The results are measured in cost of application, the control obtained and the effects on different woody plants.

In previous reports the use of large quantities of organic material as mulch on the Arboretum collections has been indicated. At various times the Arboretum has had available at low cost or simply for the hauling adequate supplies of spent hops, sawdust, wood chips, buckwheat hulls, or coffee grounds. The mulch used most recently has been cocoa shells for which there had been no commercial demand. The cocoa-shell mulch was used experimentally at first but with notable success. The mulch is fire proof, retains moisture, remains in place, i.e., does not float or blow away,

has good fertilizing value which is released slowly, and is attractive in appearance. Through staff comments to classes, publications, and the questions of many visitors a horticultural demand for this product has now been created so that gratis supplies are no longer available to us in the quantities needed. Thus, during the year it has been necessary to locate new sources of mulching material; it now appears that animal manures from local horse stables and the city zoo will be available for our needs.

In an attempt to have within the collections representatives of genera, species, varieties and cultivars offered by the nursery trade within our area, an attempt was made to locate sources for 480 advertised taxa not currently in our living collections. Many of these taxa have been tried on previous occasions and have not proved hardy; others represent new selections or new cultivars. It is desirable, however, to have information on the growth and habits of such plants, even though previous experience has shown that many may not be botanically distinguishable from already known plants or that the commercial source is unwise in offering for sale a plant which is not hardy or desirable for the Boston area. The small plants which have been obtained will be held at Weston for growth and initial hardiness tests.

One of the striking features of the Arnold Arboretum living collections is the completeness and accuracy of the labeling and mapping systems. Both of these are maintained only by constant effort. Many staff members coöperate in the continuous work of checking identifications, to insure the accuracy of the names. During the past winter a complete inventory of the plants in the living collections at Jamaica Plain and Weston was made and the nomenclature checked against Rehder's *Bibliography*, as well as more recent monographs. The work of verifying plants in the living collections from which type specimens were collected by Sargent, Rehder, and others has been continued. A special label has been prepared to identify such plants properly.

During the fall the Arboretum was approved as the National Registration authority for cultivars of woody ornamental plants not now handled by special societies. This delegation is from the American Association of Botanical Gardens and Arboreta and the American Horticultural Society and is for a two-year trial period. In this work the Arboretum staff coöperates with any individual or organization wishing to register specific groups of plants. To the present, about a dozen individuals and organizations have expressed an interest in or a willingness to carry on such registration activity. For groups not delegated to others, the members of the Arboretum staff, in an effort coördinated by Dr. Wagenknecht, will register cultivar names and compile registration lists as interest is expressed. A set of registration regulations and forms was prepared and is distributed on request. The return of these forms, plus a small registration fee, a representative herbarium specimen, and a living plant establishes the registration of a name. If a check of the literature shows that the cultivar name has not been used previously and the name is in accordance with the Inter-

national Code of Nomenclature for Cultivated Plants, the sender is so notified. Most of the plants received for registration during the first few months of this work had been given original and valid names. A few names were not acceptable, being either pre-occupied or incorrectly formed according to the Code. In each instance the sender agreed to alter the cultivar name in accordance with suggestions made. The Arboretum has no responsibility for the distinctness of the cultivar registered and legally none for the identification, although both points are of immediate concern to the staff. Where necessary, additional correspondence often has clarified the relationships of cultivars, producing information of lasting value which will be kept with the type specimen. The living plants will be kept in a special area of the Arboretum for reference and testing. If it is obvious that the species is not hardy in this area most of the registered plant material is sent to a coöperating arboretum in a more appropriate environment. The presence of authentic living and herbarium material of cultivars will facilitate the work of the staff in horticultural plant taxonomy. The end of the two-year trial period will coincide approximately with the 1962 International Horticultural Congress when steps may be taken to coördinate registration activities for all ornamental woody plants at the international level.

In the 1959 session of the Massachusetts Legislature a bill was passed to obtain from the Bussey Institution several acres of land, including that on which the Arnold Arboretum maintains its greenhouses, nursery area, hedge collection, and collection of *bonsai*. Although the bill was incorrectly filed, a new bill will be prepared. For this reason the staff has spent considerable time during this fiscal year drawing plans for new greenhouses and the necessary accessory buildings. A site was selected on land owned by Harvard University for the Arnold Arboretum along Centre Street and a program of fertilization and soil preparation is under way in this area. The new greenhouse plans will improve research facilities by providing experimental cold chambers, laboratory space and modern head-house equipment. A small classroom for graduate students and adult classes is also contemplated. The overall increase in greenhouse space will be approximately thirty-three per cent while the nursery area will be increased threefold. The President and Fellows of Harvard College, as trustees of the Arnold Arboretum, approved the plans in principle and it is expected that an architect will be selected during the summer with construction possible during the next year.

During the year the staff of the plant propagation department made a special study of the plants represented in the living collections by single specimens and those which were not in the best of condition. The unique taxa were selected for immediate propagation. Published information is lacking for the vegetative propagation of many of these and an experimental approach is necessary. In all, 257 taxa are to be considered. Initial propagation efforts have not been successful with all of these and this program will continue. Many of the plants represented by single specimens

in the collections are desirable ornamental shrubs and it is the difficulty of propagation that presumably has limited both the number of specimens which we have and their availability in trade sources.

The routine work of filling requests for plant materials and of handling shipments of seeds and plants received may occupy a large percentage of the department's work time. During the past year 245 shipments were made by air mail or air freight, parcel post and express within the United States and to twelve countries beyond. A regular exchange is maintained with most of the institutions represented. Thus, during the year, the Arboretum received 235 shipments of living material of 693 species and varieties from the same or other sources in the United States and eleven other countries. A total of fifty-two shipments of seeds representing 186 taxa was received and processed from seventeen countries, in addition to the United States. Included were many oaks and related plants and several species of blueberries from higher altitudes of southeastern Asia. A collection of seeds of *Acacia drummondii*, said to be one of the hardiest and most attractive of the acacias, was received from New South Wales. The seeds germinated well and seedlings have been distributed to locations in the South and Far West.

During the past season trees of the hardy strain of *Cedrus libani* fruited heavily. Although these plants have grown in the Arboretum for many years this clone is relatively rare in cultivation. It was possible to distribute the seed in quantity to twenty-eight locations in fourteen of the colder northern states, with shipments also going to Canada and northern Europe for trial. A replicate experiment with these seeds has shown that two months of stratification at 41° F. allowed 80% germination within four days. The seedlings are extremely susceptible to damping-off organisms, but with the rapid germination obtained it was possible to separate seedlings quickly and to minimize the spread of these diseases.

The dawn redwood, *Metasequoia glyptostroboides*, is an Arboretum introduction which has become a popular tree for general planting. While none of the plants grown from seed introduced in 1948 has yet produced staminate inflorescences, many reports of ovulate cones have been received. With no fertile seeds available the species must be reproduced by cuttings. Work during the past year revealed that cuttings taken on August 5th rooted earlier and in far better percentages than those taken on June 5th. Winter hardwood cuttings of the same plant rooted poorly.

In an experiment to determine the viability of scions in storage, crabapple scions which had been collected in December 1958 and kept in a polyethylene bag with a small amount of moistened sphagnum moss at a temperature of 41° F. were finally grafted onto appropriate stock in March 1960. Although a small number of scions was involved, the viability and successful union of most of these suggest that many materials of this kind can be stored under appropriate conditions and retained from one grafting season to the next.

The use of sulphuric acid baths to break seed coats and dormancy is

well known. Seeds of *Koelreuteria paniculata* germinated in six days following such treatment or could be stored (as in this instance) in a refrigerator for sixty days before planting. In all cases there was no evidence of the reported secondary dormancy. Seeds of *Cytisus nigricans* produced general germination in ten days following treatment in sulfuric acid for one hour. It is worth reporting that a flat of seeds of this species which had received the normal hot water treatment the previous year had failed to germinate. When these seeds were recovered and treated with sulfuric acid they, too, germinated in ten days.

Case Estates:

The house at 101 Wellesley Street in Weston adjacent to the groundcover demonstration area was made available to the Arboretum during the summer of 1959. This house, one of the oldest in Weston, was given to the Arboretum by Miss Marian Case but has been occupied by Miss Case's former gardener for a number of years. The house was reconditioned and a new heating system was installed. It is now occupied by the superintendent at the Case Estates.

The New England Daffodil Society expressed an interest in obtaining space for a test garden for *Narcissus* varieties at the Case Estates and beds were prepared for trial plots of these bulbs. The Case Estates have in various areas many naturalized bulbs which are not only colorful but draw considerable attention in the spring. A trial garden will be of value to the staff in relation to its teaching programs and to its work in cultivar registration. The New England Daffodil Society has agreed to plant and maintain the beds.

Work has continued in a general program of cleaning plantings and rejuvenating some of the older trees. Thirty old apple trees were removed during the year to reduce maintenance costs of this area and to allow for an expansion of other shrub and tree collections. Large amounts of manure were obtained without charge and many of the temporary nursery beds were fertilized following the removal of small plants.

Again this year the surplus plants were offered to the Department of Buildings and Grounds in accordance with the terms of the Arboretum trust. Approximately 450 plants of 144 taxa were offered and most of these were utilized on the Harvard campus and in conjunction with the Harvard building program.

Education:

None of the Arboretum staff was scheduled to offer formal courses at Harvard University during the past year. Several staff members assisted in the guidance of graduate students at Harvard and Radcliffe. A series of luncheon seminars for graduate students and staff was continued in which various staff members and students presented papers which were followed by discussion.

The popular classes in horticulture and botany, conducted by the staff,

were eleven in number. The field classes at Jamaica Plain and Weston continued to draw the largest numbers. Plant propagation was again enrolled to the limit of the facilities. More technical courses on plant geography, plant ecology, the gymnosperms, economic botany and a course in French on the contributions of French horticulture to American gardens drew qualified students. A course in economic botany which visited restaurants offering foreign foods proved to be a novel and appealing method of teaching. After an enjoyable meal, the class studied and discussed the plants and plant parts used for food. This course has received considerable newspaper publicity, one report even returning from Caracas, Venezuela.

Another expression of the educational activity of the Arboretum staff is found in the outside lectures which they are requested to give. Such lectures are offered at various levels. On occasion the Arboretum staff has through lectures or guided tours dealt with students from the elementary grades of the Weston schools to the graduate students of many colleges. Many requests for speakers are received from Garden Clubs and similar groups interested in horticulture. Such lectures can be both entertaining and instructive and the staff speakers attempt to make them so. Again this year approximately fifty groups numbering at least twenty-five persons were given conducted tours of the living collections in Jamaica Plain or Weston. Dr. Wood represented the Arboretum on the program of the annual Williamsburg Garden Symposium, speaking on "Birds, Bats, Bees and Botany: the Story of Pollination." Dr. Howard was a speaker on the campuses of Duquesne and Pittsburgh universities and the State University Teachers College, Oneonta, New York, under the sponsorship of the American Institute of Biological Sciences. He was the American Association for the Advancement of Sciences speaker at Franklin and Marshall College in Lancaster, Pennsylvania, and was the principal speaker for the Pennsylvania Catholic Round Table of Science at its annual meeting in Pittsburgh. Dr. Wyman was the principal speaker at the annual meetings of the Colorado Nurserymen and the Arborist Association, the Michigan Nurserymen's Association, and the Pennsylvania Nurserymen's Association. He was also the horticultural speaker at the University of Maine's Farm and Home Week and took part in the nurseryman's short course offered by the Waltham Field Station.

Exhibits and Displays:

The annual Spring Flower Show of the Massachusetts Horticultural Society was held at a new location, Wonderland Park in Revere, Massachusetts. As display space was limited, the Arboretum staff was asked to display again a pruning exhibit which was used five years ago. This exhibit, demonstrating the methods and equipment of pruning shrubs and trees, also contained examples of plants showing both correct and improper pruning. While the exhibit lacked the color of forced flowers it was awarded a gold medal. Interest in the exhibit was such that it was

again set up in the lecture hall in Jamaica Plain for the use of visitors and classes during the spring.

An open house was held at the Case Estates on May 1st to allow inspection of the nursery area, ground-cover and small-tree demonstration plots and other plantings. During the day staff members were on the grounds to answer questions. A rainy day reduced the crowds which nevertheless created a parking and traffic problem in the vicinity. As a result of such demonstrations the number of visitors and the number of tours in Weston increase each year.

A portion of the Arnold Arboretum exhibit on the grounds of the United States exhibition at the Floriade, in Rotterdam, the Netherlands, June, 1960.

From March to September, 1960, an International Horticultural Exposition, the Floriade, is being held in Rotterdam, the Netherlands. The American exhibit is under the sponsorship of the Foreign Agricultural Service of the Department of Agriculture and the American Horticultural Council. The latter organization requested the Arnold Arboretum to prepare an exhibit of plants introduced to American horticulture by the Arboretum. Dr. Wyman prepared a list which, with few exceptions, consists of plants available in European nurseries. A few plants not available in Europe were secured from our own nurseries or from commercial sources and shipped to Holland. The Arboretum plants in the American exhibit comprised part of a private arboretum as well as established landscape plantings around a typical American home. The selection

of sixty-four taxa was made to afford some bloom or point of attraction throughout the six month period of the Floriade. Elsewhere in the exhibit, the American Association of Botanic Gardens and Arboreta prepared a display of Kodachrome transparencies, photographs, and technical data, illustrating and describing American arboreta and botanic gardens. Dr. Howard served on the organizing committee, and the staff supplied pictures and details concerning the Arnold Arboretum.

The lecture hall in Jamaica Plain was again the location for temporary displays of flowering plants for classes and various special meetings. The 24th Inter-scholastic Judging and Identification Contest in Floriculture and Ornamental Horticulture was held there in April. Nearly 100 students took part in the team and individual competitions. Special displays of Arboretum plants were also prepared both at Jamaica Plain and at the Harvard Club in Boston for the annual meeting of the Associated Harvard Clubs. A special display of ornamental crab apples was prepared and exhibited at the Fall Show of the Massachusetts Horticultural Society.

Comparative Morphology:

Professor I. W. Bailey, Professor of Plant Anatomy, Emeritus, continued to serve as curator of the wood collection of the Arnold Arboretum. In addition, Professor Bailey is continuing his investigations on the comparative anatomy of the Cactaceae under a three-year grant from the National Science Foundation. Thus far, he has devoted his attention largely to the leaf-bearing genera *Pereskia*, *Pereskiopsis* and *Quiabentia*. If these putatively primitive representatives of the Cactaceae are to be utilized as an initial fundamental basis in studying salient trends of phylogenetic specialization within the family, and in obtaining evidence of valid taxonomic significance, it is essential that both the exomorphic and the endomorphic structures of all organs and parts of the three genera be thoroughly investigated.

Dr. Uttam Prakash, of the Birbal Sahni Institute of Palaeobotany, Lucknow, India, has been a visiting scholar during the year and has utilized the wood and slide collections of the Arboretum in connection with his investigations of the fossil floras of central India.

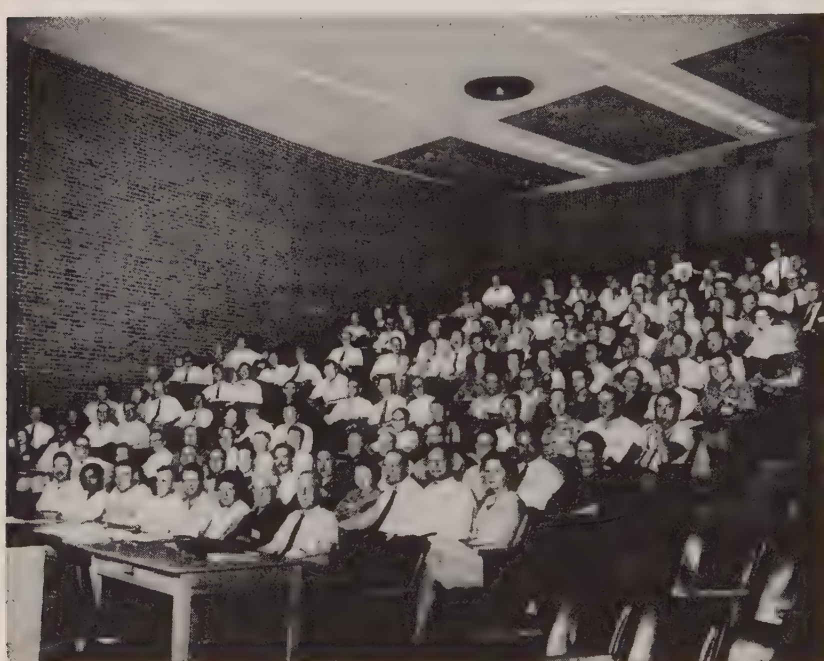
Library:

The efforts of the library staff were again concentrated on classifying and cataloguing the extensive reprint and pamphlet collection. This collection, formerly alphabetized by author as a separate unit, has now been distributed among the various library categories (e.g., monographs, floras, forestry, etc.). Three hundred fifty-six pamphlets were added to the collection, making the total number 17,340 on June 30, 1960. Two hundred sixty-eight books were added to the bound volumes bringing the total of 50,783 volumes. Fourteen hundred cards were added to the main catalogue, an indication of the extensive system of cross referencing of pamphlets and volumes now being developed.

Requests for the interlibrary loan of books remained high and 177 volumes were sent on loan from the combined libraries. An equal number of requests was handled by supplying contura copies, microfilms or photostats. The cost of such reproduction is charged to the person or institution making the request whenever possible. Filling requests in this manner requires more effort on the part of our own staff but reduces the wear on the books and allows them to remain available to our own staff.

The Gray Herbarium Index to American Plants, maintained in Jamaica Plain, received 3000 new entry cards during the year.

The Linnaean Society of London made available 825 microfiche reproductions of the Linnaean Herbarium. A set of these cards was purchased jointly with the Gray Herbarium and will be available in the library.



Meeting of the General Session on Nomenclature of the IX International Botanical Congress, which was attended by Arboretum staff members, photographed at McGill University, Montreal, Canada, on August 18, 1959.

Herbarium:

During the year 8,766 specimens were mounted and added to the herbarium, bringing the total collection to 714,136 specimens on July 1, 1960. The specimens added were in part received during the year and in part collections on hand from previous years that required study or preparation before mounting. During the past year 11,767 specimens

were received: 10,585 in exchange, 1074 by gift, 54 for special identification, and a similar number by special subsidy. The largest numbers of specimens came from institutions or collectors in Asia with 2931, 2523 and 1458 specimens from Eastern Asia, Western Malaysia and Papuasia respectively. During the year the Arboretum staff sent 1,664 specimens in exchange to other American institutions and 6,277 to institutions in other countries.

The staff filled ninety-eight requests for loans which comprised 10,903 specimens from the combined Arnold Arboretum and Gray herbaria borrowed by fifty-three different institutions, thirty-six in the United States and seventeen foreign countries from Canada to Argentina and from England to Japan. For their own work or that of students, the staff of the combined herbaria borrowed sixty loans of 5290 specimens from thirty-five institutions, sixteen in the United States and nineteen abroad. The outgoing loans averaged 111 specimens, while the incoming loans averaged 88 specimens. These figures clearly indicate the relative wealth of the herbarium collections in the Harvard herbaria and the desire of other botanists to consult this material.

The research of the herbarium staff, in part supported by special gifts and grants, involves floristic, monographic and anatomical studies. Work is in progress on the floras of the Lesser Antilles, the southeastern United States and several areas of Asia. Monographic studies of genera in Chloranthaceae, Polygonaceae, Theaceae, Thymelaeaceae and Urticaceae are progressing. Three staff members are using detailed anatomical studies for taxonomic purposes in broad surveys of plant structures and in specific scientific problems. The results of this work will be reflected in future papers similar to those cited in the bibliography of the staff.

Travel and Exploration:

During July 1959, Dr. Howard made a final trip to Hawaii in order to record growth data on some experimental projects established on the island of Kauai. On this trip he completed a report on the use and rehabilitation of agricultural lands following strip mining for aluminum ores. The report was submitted to the Commissioner of Public Lands and was used for reference in preparing mining-rehabilitation legislation for the state of Hawaii. During two weeks of December and January, Dr. Howard and Dr. Wagenknecht collected in Florida, Jamaica and the Cayman Islands. The primary purpose of this trip was to observe agricultural and forest plantings on mined-out bauxite lands in Jamaica. The opportunity was taken to collect specimens of cultivated ornamental shrubs and trees in all three areas.

The Arboretum contributed to the support of the expedition of Drs. Ernst and Lucy Abbe, of the University of Minnesota, to Thailand, Cambodia, the Malay Peninsula, and Borneo. The purpose of this expedition was a study of the Asiatic oaks and their relatives. Dr. Abbe sent acorns and other fruits from the mountain areas for trial at the Arboretum

where some species from the area are now under cultivation. Approximately a thousand collection-numbers of herbarium specimens were gathered by this expedition.

Gifts and Grants:

During the spring the Arboretum was notified that it had been designated as one of three beneficiaries of a perpetual charitable trust fund established under the will of Mrs. Martha Dana Mercer, of Doylestown, Pennsylvania, a long-time friend of the Arboretum, who died February 21, 1960. The fund is being handled by the Old Colony Trust Company of Boston with the income to be paid to the Arnold Arboretum. The use of this generous gift is unrestricted, and the income when available will be applied to improvement of the physical facilities and for increases in the staff of the Arboretum.

Again this spring the "Friends of the Arnold Arboretum" were generous in their response to the annual appeal for gifts to support the horticultural activities of the Arboretum. Even though such gifts are, with few exceptions, unrestricted they have been used for the most part in the areas of plant propagation and the care of the living collections.

Special gifts or grants from individuals and foundations were received to support the research of various staff members. A gift from Mr. George R. Cooley will support the collaborators of Dr. Wood on the flora of the southeastern United States. In addition, Dr. Reed C. Rollins, Director of the Gray Herbarium, and Dr. Wood received a three year grant from the National Science Foundation for the preparation of a biologically oriented generic flora of the southeastern United States. Dr. Perry received a one year grant from the Public Health Service for investigations on the native medical uses of plants of southeastern Asia. This grant, which may be renewed twice, is utilizing the extensive herbarium collections of the Arnold Arboretum from that area. Grants from the National Science Foundation to Dr. Bailey and Dr. Howard for their research have been continued.

Publications:

Under the editorship of Dr. Wyman, Volume 20 of *Arnoldia* was issued during the year. As a policy the articles in *Arnoldia* are of timely horticultural interest. The issues appear at irregular intervals with twelve numbers comprising each volume. The *Journal of the Arnold Arboretum*, by contrast, is issued quarterly on a regular basis with technical articles largely representing the research of the staff members. Volume 40 of the *Journal* was issued during 1959.

Dr. Wyman advised and coöperated with the Electric Council of New England in the publication of a twenty-four-page booklet, "Trees in Your Community — A Handbook of Selected Trees for New England." The recommendations were often based on growth habits of trees observed in our own small-tree demonstration plot in Weston and on the Arboretum

grounds in Jamaica Plain. The booklet is being distributed by New England wire-using utilities to home owners interested in the subject. Orders for 156,000 before printing indicate the need and popularity of such handbooks.

Bibliography of the Published Writings of the Staff and Students July 1, 1959 — June 30, 1960

BAILEY, IRVING WIDMER. Some useful techniques in the study and interpretation of pollen morphology. Jour. Arnold Arb. **41**: 141–148. 1960.

HOWARD, RICHARD ALDEN. An additional note on *Tillandsia paniculata*. Bromeliad Soc. Bull. **9**: 54–56. 1959.

———. The Director's Report. The Arnold Arboretum during the fiscal year ended June 30, 1959. Jour. Arnold Arb. **40**: 420–436. 1959.

———. Studies in the genus *Coccoloba*, VII. A synopsis and key to the species in Mexico and Central America. Jour. Arnold Arb. **40**: 205–220. 1959.

———. Studies in the genus *Coccoloba*, VIII. Nomenclatural changes. Jour. Arnold Arb. **41**: 40–46. 1960.

———. Studies in the genus *Coccoloba*, IX. A critique of the South American species. Jour Arnold Arb. **41**: 213–229. 1960.

HU, SHIU-YING. Chinese hollies. Tsing Hua Jour. Chinese Stud. Spec. No. Nat. Sci. **1**: 150–184. 1959.

———. A monograph of the genus *Paulownia*. Quart. Jour. Taiwan **12**: 1–54. 1959.

———. A revision of the genus *Clethra* in China. Jour. Arnold Arb. **41**: 164–190. 1960.

JOHNSTON, IVAN M. Some noteworthy American Borages (Studies in the Boraginaceae, XXX). Wrightia **2**: 13–22. 1959.

KOBUSKI, CLARENCE E. A revised key to the Chinese species of *Jasminum*. Jour. Arnold Arb. **40**: 385–390. 1959.

NEVLING, LORIN I., JR. Araliaceae. *In*: Woodson, R. E. *et al.* Flora of Panama. Ann. Missouri Bot. Gard. **46**: 223–242. 1959.

———. A revision of the genus *Daphnopsis*. Ann. Missouri Bot. Gard. **46**: 257–358. 1959.

SAX, KARL. The cytogenetics of facultative apomixis in *Malus* species. Jour. Arnold Arb. **40**: 289–297. 1959.

———. Meiosis in interspecific pine hybrids. Forest Sci. **6**: 135–138. 1960.

———. Standing room only. (Revised paperback edition.) Boston. 1960.

SCHWARTEN, LAZELLA. Index to American botanical literature. Bull. Torrey Bot. Club **86**: 147–157, 206–217, 270–282, 353–365. 1959; **87**: 73–83, 161–171, 229–245. 1960.

THOMAS, JOAB. A monographic study of the Cyrillaceae. Contr. Gray Herb. **186**: 1–114. 1960.

WAGENKNECHT, BURDETTE L. Christmas plants around the world. Arnoldia **19**: 59–77. *pl. 10–13*. 1959.

———. Note on *Elaeagnus commutata*. Rhodora **62**: 29. 1960.

———. Revision of *Heterotheca*, section *Heterotheca* (Compositae). Rhodora **62**: 61–76, 97–107. 1960.

WATERMAN, ANN H. The mints (family Labiatae) of Michigan. Mich. State Univ. Biol. Ser. **1**: 271–302. 1960.

WEBER, CLAUDE. Botanical motifs of the coats of arms on stamps. Topical Times **11**: 14–19. 1959.

———. National flowers and trees on stamps. Topical Times **10**: 200–202. 1959.

———. Palms on postage stamps. Principes **4**: 9–16. 1960.

WILSON, KENNETH A. The genera of Hydrophyllaceae and Polemoniaceae in the southeastern United States. Jour. Arnold Arb. **41**: 197–212. 1960.

———. The genera of the Arales in the southeastern United States. Jour. Arnold Arb. **41**: 47–72. 1960.

———. The leptosporangium of the New Zealand fern *Anarthropteris dictyopteris*. Contr. Gray Herb. **187**: 53–59. 1960.

———. The sporangia of three problematic species of *Polypodium*. Am. Fern Jour. **49**: 147–151. 1959.

——— (with C. E. WOOD, JR.). The genera of Oleaceae in the southeastern United States. Jour. Arnold Arb. **40**: 369–384. 1959.

WOOD, CARROLL E., JR. The genera of Sarraceniaceae and Droseraceae in the southeastern United States. Jour. Arnold Arb. **41**: 149–163. 1960.

———. The genera of Theaceae in the southeastern United States. Jour. Arnold Arb. **40**: 413–419. 1959.

——— (with R. B. CHANNELL). The genera of the Ebenales in the southeastern United States. Jour. Arnold Arb. **41**: 1–35. 1960.

———. The genera of Plumbaginaceae in the southeastern United States. Jour. Arnold Arb. **40**: 391–397. 1959.

———. The genera of the Primulales of the southeastern United States. Jour. Arnold Arb. **40**: 268–288. 1959.

——— (with K. A. WILSON). The genera of Oleaceae in the southeastern United States. Jour. Arnold Arb. **40**: 369–384. 1959.

WYMAN, DONALD. The dwarf evergreens. Horticulture **37**: 472, 473, 485, 486. 1959.

———. Few hawthorns selected from numerous species. Am. Nurseryman **110**(9): 10, 11, 98–101. 1959.

———. Firs contribute stately specimens to northern gardens. Am. Nurseryman **110**(11): 12, 13, 70–72. 1959.

———. Hydrangeas include old favorites in limited list of garden species. Am. Nurseryman **110**(3): 14, 15, 53–55. 1959.

———. Magnolias hardy in the Arnold Arboretum. Arnoldia **20**: 17–28. 1960.

———. Many forms and uses rank maples high among shade trees. Am. Nurseryman **110**(7): 10, 11, 88–94. 1959.

———. Maples liven the autumn scene. Horticulture **37**: 512, 513, 541. 1959.

———. Plant introduction by the Arnold Arboretum. Bull. Univ. Wash. Arb. **22**: 74–76, 100. 1959.

———. Plants of possible merit? Arnoldia **20**: 9–16. 1960.

———. Shrub honeysuckles with pink to red flowers. Arnoldia **20**: 29–32. 1960.

———. Sorting the woody ornamentals — Dogwoods yield varied foliage, flowers, fruits. Am. Nurseryman **111**(9): 10, 11, 105–111. 1960.

———. Sorting the woody ornamentals — Few spireas popular despite range in height and blooming time. Am. Nurseryman **111**(11): 10, 11, 71–76. 1960.

———. Sorting the woody ornamentals — Magnolias provide flowering trees for almost all sections. Am. Nurseryman **111**(7): 12, 13, 69–80. 1960.

———. Sorting the woody ornamentals — *Philadelphus* popular for spring white. Am. Nurseryman **111**(5): 14, 15, 68–73. 1960.

———. Sorting the woody ornamentals — A second look at the popular elm. Am. Nurseryman **111**(1): 12, 13, 78–82. 1960.

———. Sorting the woody ornamentals — The variable *Euonymus*. Am. Nurseryman **111**(3): 16–18, 93–96. 1960.

———. These make spring focal points. Horticulture **38**: 207. 1960.

———. Viburnums. Arnoldia **19**: 47–56. 1959.

———. Viburnums valued for varied species useful in gardens. Am. Nurseryman **110**(5): 14, 15, 61–71. 1959.

———. *Weigela* list reflects changing styles. Am. Nurseryman **110**(1): 12, 13, 30–33. 1959.

———. Why not plant many viburnums? Horticulture **37**: 34, 35, 41. 1960.

RICHARD A. HOWARD, *Director*

Staff of the Arnold Arboretum
1959–1960

RICHARD ALDEN HOWARD, Ph.D., Arnold Professor of Botany, Professor of Dendrology, and Director.

IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus.*
JOSEPH HORACE FAULL, Ph.D., Professor of Forest Pathology, *Emeritus.*
KARL SAX, S.D., Professor of Botany, *Emeritus.*

MICHAEL ANTHONY CANOSO, M.S., Curatorial Assistant.*
ANN CLOSE, A.B., Business Secretary.**
HENRY DRAPER, Superintendent, Case Estates.
ALFRED JAMES FORDHAM, Propagator.
HEMAN ARTHUR HOWARD, Assistant Horticulturist.
SHIU-YING HU, Ph.D., Botanist.
FRANCES MARY JARRETT, Ph.D., Botanist.
IVAN MURRAY JOHNSTON, Ph.D., Associate Professor of Botany.
CLARENCE EMMEREN KOBUSKI, Ph.D., Curator.*
MARGARET CATHERINE LEFAVOUR, Herbarium Secretary.
MARY SCANLAN LEHMER, Ed.M., Business Secretary.***
SUSAN DELANO MCKELVEY, A.B., Research Associate.
LORIN I. NEVLING, JR., Ph.D., Assistant Curator.
LILY MAY PERRY, Ph.D., Botanist.
LAZELLA SCHWARTEN, Librarian.*
JOAB LANGSTON THOMAS, Ph.D., Cytotaxonomist.
BURDETTE LEWIS WAGENKNECHT, Ph.D., Horticultural Taxonomist.
ANN H. WATERMAN, M.S., Assistant Librarian.*
CLAUDE WEBER, Botanist, Special Project.*
KENNETH ALLEN WILSON, Ph.D., Botanist, Southeastern Flora Project.*
ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator and Editor.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium
** Appointed June 15, 1960
*** Resigned June 15, 1960

INDEX